ASPECTS OF THE ENERGETICS OF THE COCKLE *CHIONE (AUSTROVENUS) STUTCHBURYI* IN THE AVON-HEATHCOTE ESTUARY, CHRISTCHURCH, NEW ZEALAND

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ABSTRACT

Aspects of the energetics of the cockle *Chione (Austrovenus) stutchburyi* in the Avon-Heathcote Estuary, Christchurch, New Zealand. R.L. Stephenson. Department of Zoology, University of Canterbury, Christchurch, New Zealand. 1981.

Aspects of the energy flow through *Chione (Austrovenus) stutchburyi* (Wood, 1828), a major member of the benthic macrofaunal community of the Avon-Heathcote Estuary, are investigated in order to define the role of this species and to test the hypothesis that this animal has a major role in the energy flow of the entire system.

An historical account of the small (6 km^2 area), shallow, mainly intertidal, bar-built, Avon-Heathcote Estuary (44°33'S, 172°44'E) documents the alteration in physical and biological characteristics with the expansion of the city of Christchurch within its drainage basin.

In an introduction to the cockle, the nomenclature is discussed, and a description of larval development of *C. stutchburyi* reared in the laboratory is presented.

The distribution of *C. stutchburyi* in the Avon-Heathcote Estuary was analysed from a survey of 200 sites. Relationships between size, weight and age, based upon 1000 individuals, allowed estimates of biomass and production; and their spatial distribution. Distribution is shown to be limited to levels on the shore with greater than 1.5 hours of water cover per tide and to sediments containing less than 50% mud and a mean sand diameter smaller than 2.25 Ø. Preference of *C. stutchburyi* for greater than nine hours of water cover per tide, 10-30% mud content of the sediment, 2.5 - 3.0 Ø mean sand diameter and 2.7 Ø median sand diameter was assessed by analysis of the distribution of biomass and density.

Density manipulation field experiments were conducted in an attempt to define the magnitude and distribution of recruitment, and to investigate the response of adult populations to disturbance and changes in density.

Energy budget calculations for *C. stutchburyi* show a total winter biomass of 8.2×10^7 to 1.7×10^9 g in the Avon-Heathcote Estuary (energy content of 1.62×10^9 to 3.4×10^{10} kJ). On an areal basis, energy assimilated is estimated to be 4.3×10^2 to 4.7×10^3 kJ m^{-2} yr^{-1}; between

respiration (96.7 - 2.0 × 10^3 kJ m^{-2} yr^{-1}) and total production (3.3 × 10^2 - 2.7 × 10^3 kJ m^{-2} yr^{-1}). Total production is partitioned into production of body growth (32.2 - 2.0 × 10^2 kJ m^{-2} yr^{-1}), production of reproductive products (1.1 × 10^2 - 2.3 × 10^3 kJ m^{-2} yr^{-1}) and mortality (2.0 × 10^2 kJ m^{-2} yr^{-1}).

A stable carbon isotope study of *C. stutchburyi* and possible food sources revealed a range in $\delta^{13}C$ values of cockle tissue in parts of the population separated by less than two km, but subject to different hydrological regimes. This is clearly attributable to differences in the marine and terrestrial contributions of carbon to the suspended particle load (and therefore the diet), and proves that *C. stutchburyi* utilises allochthonous organic carbon from the drainage basin, as well as marine carbon.

Energy flow through the entire estuary (calculated by the energy analysis methods of H.T. Odum) is estimated to be approximately 8.1 × 10^9 kJ m^{-2} yr^{-1}. The physical energy in flows of freshwater and the tide is the most significant contribution, followed by nutrient energy input from the Bromley Oxidation Ponds and the chemical energy of seawater dilution by freshwater.

Two models of energy flow through *C. stutchburyi* and other major compartments of the Avon-Heathcote Estuary are presented and used to simulate the removal of oxidation pond discharge. From these models it is concluded that a significant proportion of the cockle population may be supported by the energy in pond discharge.

Although the total energy flow through the *C. stutchburyi* population is small in comparison to that of the whole estuary (3.0 × 10^{-5}%), the cockle is concluded to be especially important to the energetics of the entire estuary because of the high connectivity with other components of the system, and its intimate association with the particulate organic matter food chain.

1. GENERAL INTRODUCTION

1.1 RATIONALE

1.1.1 The Concept of Community Energetics

The study of animal communities has progressed from the identification of component species to the assessment of relationships between species, communities and their environments (Nichols, 1975).

Definitions of ecology such as:

(1) "the study of the relationships between structure and function in nature" (E.P. Odum, 1968),

(2) "the search for principles to understand nature" (H.T. Odum pers. comm., 1979), and

(3) "the study of interactions and relationships between living systems and environment" (F.B. Golley - preface to Wiegert, 1976)

have demanded that components of ecosystems be considered and studied together rather than in isolation.

In an attempt to equate ecosystem components and to express all terms in comparable units, energy (i.e. the calorie) has been used as the common denominator. The field of ecological energetics consisting of studies of trophic transfer and transformation of energy through populations and communities (Wiegert, 1976) has developed as a major theme in ecology.

Ecological energetics developed as an entity from the ecosystem concepts which were developed during the first four decades of the twentieth century (E.P. Odum, 1968; Wiegert, 1976) and this is outlined below.

Forbes (1887) in his qualitative description of the aquatic food web linked the living and non-living components of the lake ecosystem (microcosm). In the 1920's the terms "producers" and "consumers" were introduced by Thieneman (1926, cited in E.P. Odum, 1968), and Elton (1927) recognised the organisation of the food chain into a "pyramid of numbers". Juday (1940), recognising the input of solar radiation as the principal factor in determining the physical, chemical and biological cycle of changes that take place within the water, considered both the physical and

biological components of the lake in terms of their energy content. Lindeman in "The trophic dynamic aspect of ecology" (1942) presented the idea that components of an ecosystem could be linked by flows of energy through a food web or trophic pyramid.

With increasing awareness of the role of trophic feeding levels came an appreciation of the significance of standing crop and the turnover rate of biomass, rather than just numbers, in describing and comparing the functional state of ecosystems (Wiegert, 1976). Comparisons were made of the production of biomass per unit time and Macfadyen (1948) summarised and discussed the concept and meaning of productivity in biological systems.

During the 1960's, several papers were published documenting calorific (energy) values of the components of ecosystems (for example Golley, 1961; Slobodkin & Richman, 1961; E.P. Odum *et al.*, 1965; Cummins, 1967; Cummins & Wuycheck, 1971; Schroeder, 1977) and by the time of Phillipson's book (1966), the pattern of energetic studies as a quantitative description of energy flow had been established, based upon the equation:

energy content of food assimilated	=	energy content of tissues produced in growth	+	energy degraded and lost as heat of respiration.

During the IBP programme (1964-1974), energy flow formed the basic theme of studies of production and productivity in a wide variety of ecosystems. Significant advances were made in techniques, and several IBP handbooks form the basis of present terminology, methods, and conventions in ecological energetics (see for example Petrusewicz & Macfadyen, 1970; Crisp, 1971; Grodzinski *et al.*, 1975).

Ecological energy transformations can be described by the equation:

$$C = P + R + F + U$$

where in energy terms;

C (consumption)	=	Intake of food,
P (production)	=	Energy content of the biomass of material directed toward body growth (material assimilated less that respired or rejected),
R (respiration)	=	Energy lost as heat in life processes (maintenance),
F (faeces/egesta)	=	Energy content of that part of consumption which is not assimilated, and

U (urine/excreta) = Energy content of that part of the digested material that is passed from the body (excluding reproductive and secretory products)

(after Grodzinski *et al.*, 1975).

The concept of the energy budget has been unifying in its effect on the study of communities, for it has allowed quantitative expression of relationships from a molecular and biochemical level, to a physiological and ecological level all with a common denominator (energy); and this has formed the basis for the creation of community models to describe and equate relationships between components of ecosystems.

After 1950, studies in ecological energetics developed along two lines (Wiegert, 1976). One approach emphasised energy flow through trophic levels of ecosystems and demonstrated that important generalisations (such as of gross and net production, exported production etc.) could be derived from measurements of the metabolism of whole communities (H.T. Odum & E.P. Odum, 1955; H.T. Odum, 1957; Teal, 1957; etc.). Consideration of energetics of entire systems or of single species led to estimation of parameters of system efficiency (H.T. Odum & Pinkerton, 1955; Margalef, 1963; Golley, 1968; McNeill & Lawton, 1970) for example production/respiration (P/R) ratios, and formed the basis for quantitative comparison of ecosystems.

The other approach dealt with energy dynamics of single populations or food chains, including those in experimental laboratory conditions (for example: Richman, 1958; Slobodkin, 1959). Advancements were being made in the application of physiological techniques to energetics, notably in the measurement of respiration (e.g. E.P. Odum & Smalley, 1959; Golley, 1960; E.P. Odum *et al.*, 1962; Phillipson, 1962) and in rates of uptake, elimination and flux of food energy using radioactive tracers (e.g. Crossley & Howden, 1961; E.P. Odum & Golley, 1963; Reichle, 1967; Wiegert *et al.*, 1967). Generalisations became apparent in the range of variation of energy budget parameters and were documented in several groups of animals (assimilation and respiration in man, Kleiber, 1961; respiration in orders of birds, Zar, 1968; relationships between assimilation efficiencies of aquatic consumers, Welch, 1968; production efficiencies of ectotherms, Humphreys, 1978; production and respiration, May, 1979; Humphreys, 1979).

Energy budgets of numerous individual organisms and species are now found in the literature and have allowed the study of the following topics to be developed:

(a) assessment of techniques and comparison of methods (e.g. respirometry (Wightman, 1977) and calorimetry (Schroeder, 1977));

(b) evaluation of the ecological significance of measured components of an energy budget (Welch, 1968; Klekowski, 1970; Robertson, 1979; Wightman, 1977, in prep.); and

(c) the physiological control of energetic parameters (Calow, 1977; Bayne *et al.*, 1975a, 1975b; Newell *et al.*, 1977).

Studies of the energetics of whole systems has contributed to the rapidly expanding field of ecosystem modelling. A recent advance has been the approach to "energy analysis" by H.T. Odum and co-workers (H.T. Odum, 1971, 1972, 1978, in press; H.T. Odum & E.C. Odum, 1976; Hall & Day, 1976). Energy analysis is the modelling of systems accompanied by an evaluation of the energy flows inherent in the system, and has been used as the basis for the comparison and management of complex systems. This method includes a synthesis of ecosystem components into whole patterns, where energy flow is used as the common unit of measurement among parts. It is unique in allowing the direct comparison of energy flows of different types using energy quality ratios, so that pathways may be compared to determine their relative significance in relation to each other and to energy flow through the entire system (see section 5.1). Community energetics forms a convenient framework within which to investigate aspects of the structure and function of ecosystems.

1.1.2 The Role of One Species in the Energetics of an Entire Ecosystem

Studies of the energetics of individual organisms and species commonly have been undertaken with the view that they would help elucidate the patterns of energy flow in the system involved (e.g. Kay & Brafield, 1973) and that they would allow evaluation of the relative importance of a species population in an ecosystem (e.g. Hibbert, 1977). Marine intertidal molluscs have featured in such energetic studies [for example the gastropods *Littorina irronata* (E.P. Odum & Smalley, 1959), *Tegula funebralis* (Paine, 1971), three species of *Nerita* (Hughes, 1971a); the limpet *Fissurella barbadensis* (Hughes, 1971b); the bivalves *Modiolus demissus* (Kuenzler, 1961), *Scrobicularia plana* (Hughes, 1970), *Crassostrea virginica* (Dame, 1976; Bahr, 1976), *Mercenaria mercenaria* (Hibbert, 1976, 1977a, 1977b)].

While such studies have provided essential data on the role of these species; in general, they have not been accompanied by enough detail of the energy characteristics of the whole system to allow the magnitude of their role to be assessed. In most cases, results are compared with other species for which energy budgets have been completed, or to similar animals in other situations in order to assess their relative magnitude.

On the other hand, whole ecosystem models (many of which have been of coastal marine and estuarine areas; e.g. H.T. Odum, 1957; Teal, 1962; Riley, 1963; Steele, 1974; Cronin, 1975; Nihoul, 1975; Patten, 1971-5; Hall & Day, 1977; Kremer & Nixon, 1978) are by necessity simplified (Kremer & Nixon, 1978) and lack the detail of energy estimates needed to assess the role of particular species.

To assess the role of a species in an ecosystem properly, the energy budget of that species needs to be compared with the magnitude of the energy flow through the whole system. Only now is this becoming a feasible proposition; with improved precision in the measurement of parameters of energy budgets, greater understanding of the physiological variability involved, and a large accumulated data base at an individual and species level - combined with the considerable advancements that have been made in estimating the energy flows of entire systems.

This study is an attempt to make such an assessment of the energetics of the cockle *Chione (Austrovenus) stutchburyi* in a small estuary, to test the hypothesis that this prominent member of the benthic macrofaunal assemblage has a major role in energy flow through the system.

The Avon-Heathcote Estuary system is described in section 1.2 and the cockle *Chione (Austrovenus) stutchburyi* is introduced in 1.3. Section 2 deals with the distribution of *C. stutchburyi* in the Avon-Heathcote Estuary including the distribution of density and biomass, and a discussion of the factors influencing distribution. The population dynamics of *C. stutchburyi* are discussed in section 3, including the results of density manipulation experiments. A traditional energy budget is calculated for *C. stutchburyi* in section 4. The total energy flow through the Avon-Heathcote Estuary is estimated in 5.1, two simulation models of energy flow through *C. stutchburyi* are presented in 5.2 and the role of the cockle in the estuary is assessed in the synthesis (section 6).

1.2 THE AVON-HEATHCOTE ESTUARY

1.2.1 Physical Description

The Avon-Heathcote Estuary is a small (6 km^2 area) bar-built estuary on the east coast of South Island, New Zealand (43°33'S, 172°44'E) (Fig. 1.1, 1.2).

It is microtidal (spring tide range = 2.1 m), shallow (mean depth at HWOST = 1.4 m), predominantly intertidal (85% of the area is intertidal mudflat), weather (wind) dominated and well mixed with over 56% tidal exchange per tide (Knox & Kilner, 1973; Macpherson, 1978).

The bed of the Avon-Heathcote Estuary consists largely of fluvial silt with some deposition of sand near the mouth. It is flanked on its three sides by areas of completely different geomorphological character: to the west the flat swampy areas of alluvial silt and fluviatile gravels, peat and dune remnants of the Canterbury Plains; to the south the volcanic mass of Banks' Peninsula, and to the east the sandy New Brighton spit, separating the estuary from the South Pacific Ocean (Macpherson, 1978).

Two rivers, the Avon and the Heathcote, serve a drainage basin of approximately 200 km^2 within which the city of Christchurch is located. About 85% of the catchment is less than 30 m above mean sea level, and about 80% of this area is currently urbanised (Scott, 1963; Macpherson, 1978) (Fig. 1.1).

The Avon-Heathcote Estuary has been the subject of a significant amount of research; especially in the last 15 years. Interest in hydrology (especially with respect to flooding in the city) initiated by the Christchurch Drainage Board has resulted in detailed studies of hydraulics (Hydraulics Research Station Wallingford 1970, 1972 a, b), sediments (Macpherson, 1978) and ecology of the Avon-Heathcote Estuary (Knox & Kilner, 1973); and these reports form an adequate physical description of the present estuary and review of previous studies.

The present hydrology of the Avon-Heathcote Estuary is summarised in Fig. 1.3. Dry weather flows from the Avon and Heathcote Rivers contribute 4.4 $m^3\ sec^{-1}$ of fresh water to the estuary, and treated sewage and other minor inflows add another 1.5 $m^3\ sec^{-1}$. During storms with a five year return period, river inflows increase to 60 $m^3\ sec^{-1}$ (Mawson, 1972; Macpherson, in press b).

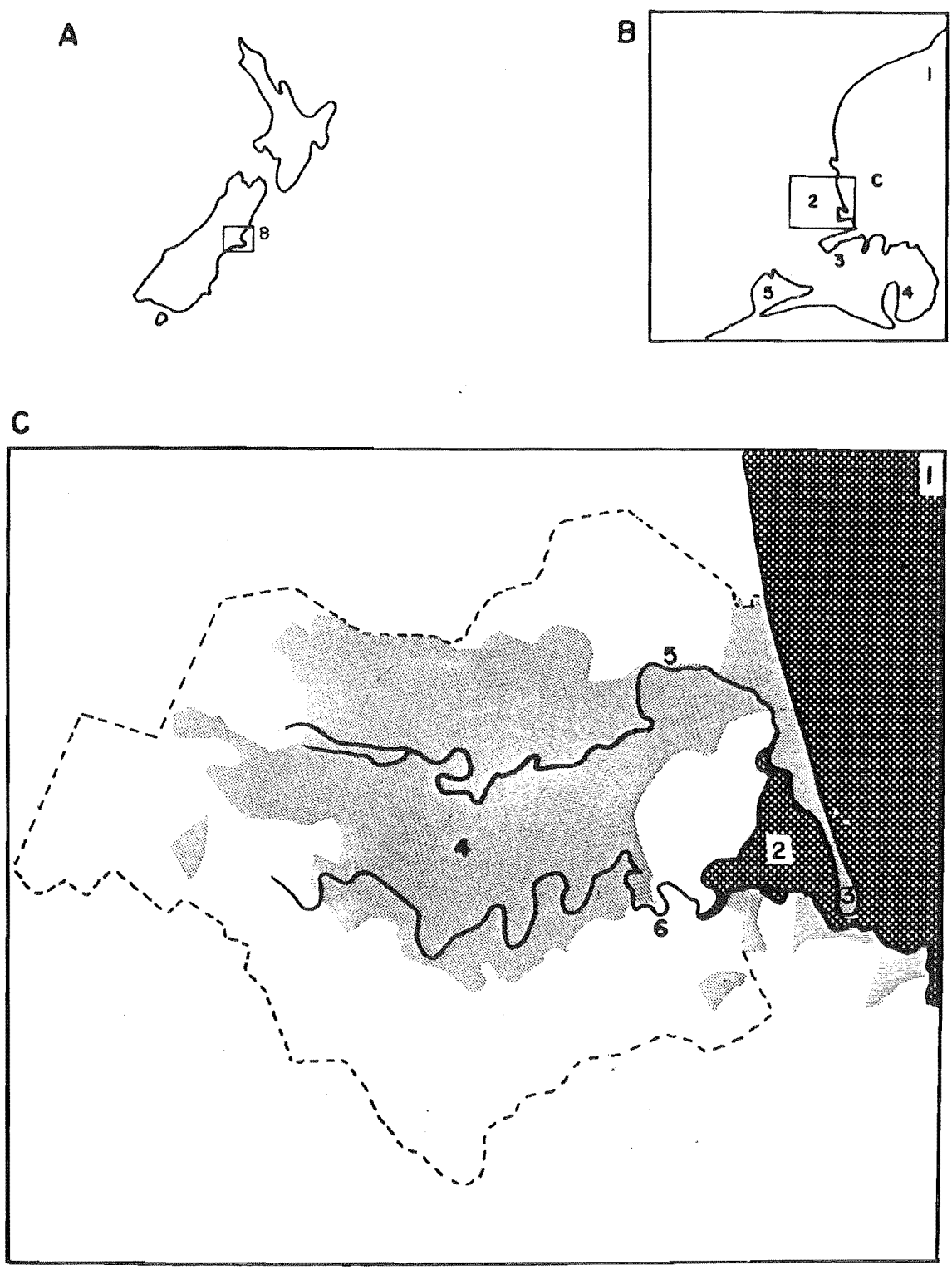

Fig. 1.1 Location of the Avon-Heathcote Estuary. A, New Zealand showing location of Banks Peninsula. B, Banks Peninsula and the Canterbury Plains: 1, Pegasus Bay; 2, location of Christchurch; 3, Lyttelton Harbour; 4, Akaroa Harbour; 5, Lake Ellesmere. C, the Avon-Heathcote Estuary and its catchment (dotted line): 1, Pegasus Bay; 2, Avon-Heathcote Estuary; 3, South Brighton Spit; 4, Christchurch (shaded) urban area; 5, Avon River; 6, Heathcote River.

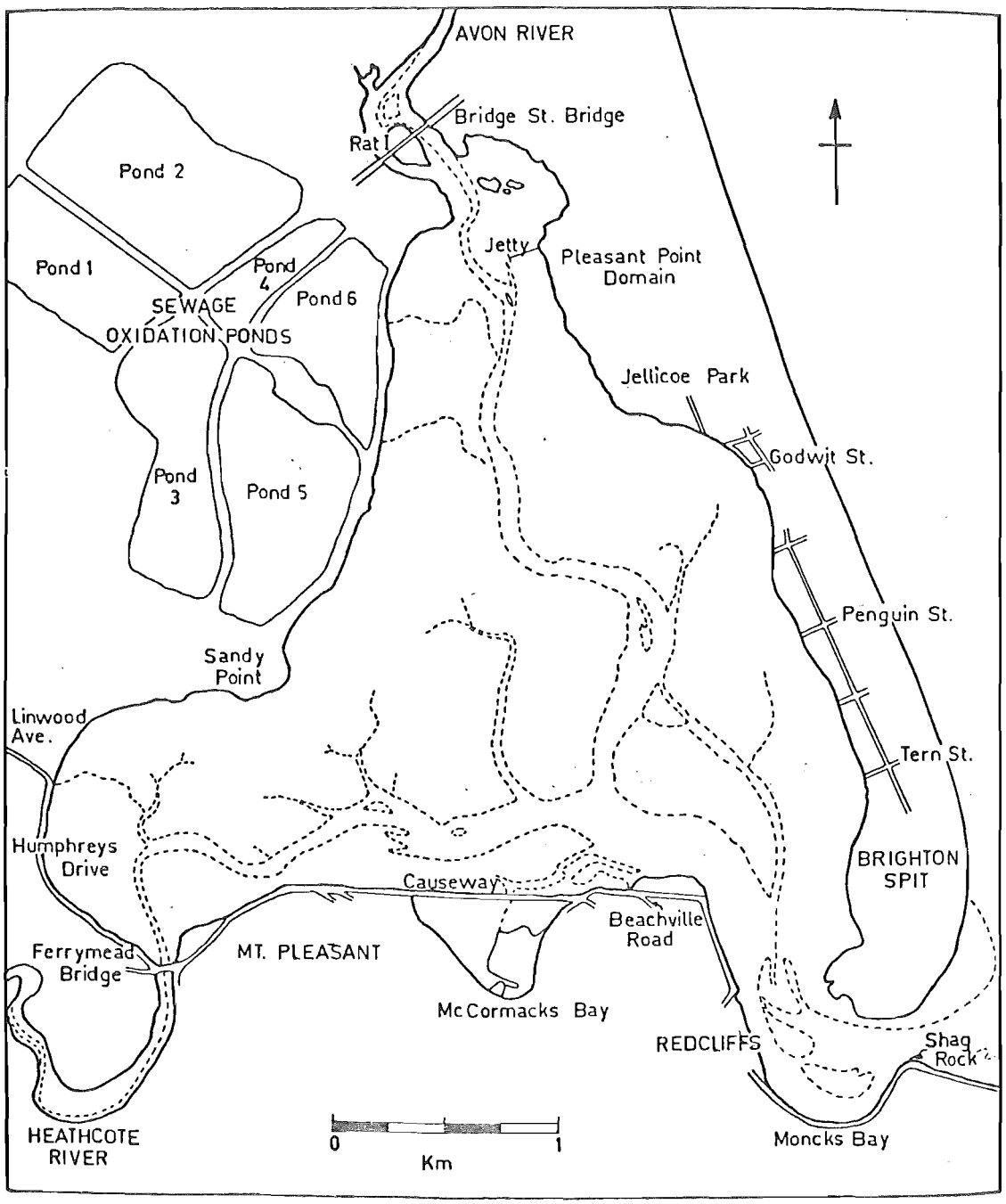

Fig. 1.2 Map of the Avon-Heathcote Estuary showing locations mentioned in the text.

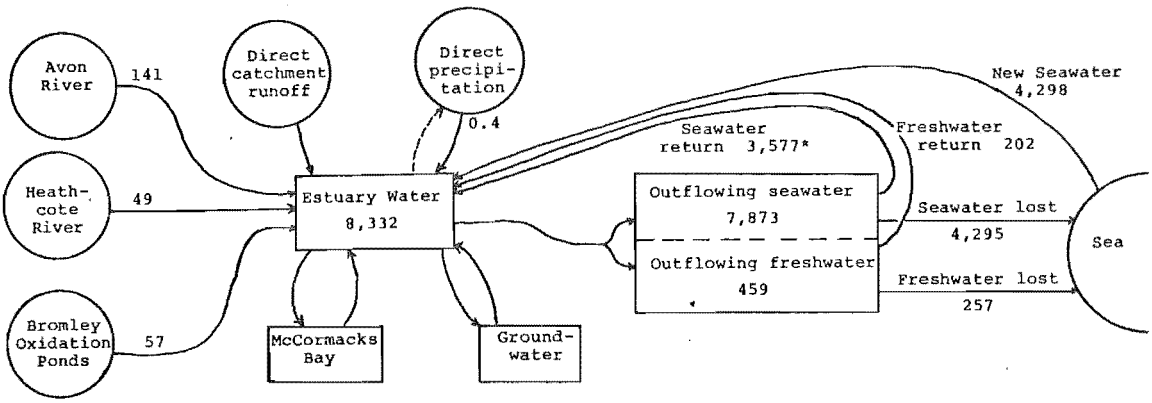

Fig. 1.3 Hydrology of the Avon-Heathcote Estuary in mean tide volumes ($m^3 \times 1000$). Sea water return calculation (*) based upon 44% return of fresh water (Knox & Kilner, 1973).

1.2.2 Historical Perspective

During the past 130 years, the city of Christchurch has grown within the drainage basin to the present population of approximately 300,000 and the effect that this urban and industrial development around the estuary has had upon the estuarine ecosystem has been significant. The Avon-Heathcote Estuary has reflected the drastic alteration of its drainage basin by changes in its own physical, chemical and biological characteristics. Changes in vegetation, drainage patterns and land cover have altered the nature and degree of flow characteristics and sedimentation. In addition, domestic and industrial effluents discharged into the rivers and into the estuary proper have had far-reaching effects upon the kinds and numbers of plants and animals within the estuary (Thompson, 1930; Hercus, 1942; Bruce, 1952; Scott, 1963; Knox & Kilner, 1973). In parallel with these man-induced changes there have been naturally occurring, short-term changes in the configuration of the spit, the outlet channel and channels within the estuary, characteristic of estuarine instability.

European settlement of the drainage basin began in the 1850s. At that time, flats forming the catchments of the two rivers and their tributaries were largely areas of swamp. Raupo *(Typha muelleri)* and flax *(Phormium tenax)* were dominant; interspersed with tussock grass, fern, tutu *(Coriaria* sp.) and patches of swamp forest dominated by kahikatea *(Podocarpus dacrydoides)* (Knox & Kilner, 1973). Early maps show many shallow ponds and shaking bogs, drained by a dense network of small meandering streams, and separated from the sea by a belt of low dunes (Scott, 1963).

Growth of the city was rapid, both in terms of population and in the area of the drainage basin urbanised (Fig. 1.4A). As the population grew, the quality of the watershed surface water deteriorated (Hercus, 1942; Scott, 1963) to the point where after rain the area was often a "... pestilential swamp" (Hercus, 1942). Although early drainage works were undertaken by the Canterbury Provincial Council, it was not until 1878, after the formation of the Christchurch Drainage Board, that an organised start was made on an underground stormwater and sewage system (Hercus, 1942). This effluent was subjected to primary treatment at the Bromley Sewage Farm before being discharged into the estuary. Raw sewage passed through a settling tank from which liquid ran across the paddocks of the farm to the estuary. The amount of sewage that was produced was too great for the number of filter paddocks available, and some effluent was run into a ponding area where it underwent purification by oxidation and bacterial action before entering the estuary (Bruce, 1952). This resulted in improved quality of surface water and in 1890 the Colonial Analyst reported that water entering the estuary from the sewage farm was "... deprived of any harmful constituents" (Hercus, 1942).

By 1901, 54 km of pipes were laid (Fig. 1.4B) and 12.1×10^6 litres of effluent flowed daily into the sewage farm. A side effect of the sewage system was a change in surface run-off characteristics of the drainage basin. By 1930, a minimum of 7.2×10^3 l ha^{-1} dy^{-1} of ground water entered the sewers from the city area (Scott, 1963), reducing surface run-off from unpaved areas as a result (Macpherson, 1978).

Although the sewage farm served the city itself, untreated domestic effluent entered the estuary from several surrounding housing areas. Most significant, however, was the discharge of industrial effluents directly into the estuary and its rivers. The area of Woolston, along the banks of the Heathcote River, became the most heavily industrialised area of New Zealand (with one-fifth of the total New

Zealand work force employed in the area in 1903) and the estuary received the (often untreated) effluent from factories, including woollen mills, rubber factories, a gelatine and glue factory, woolscouring works, a fellmongery, and a starch factory.

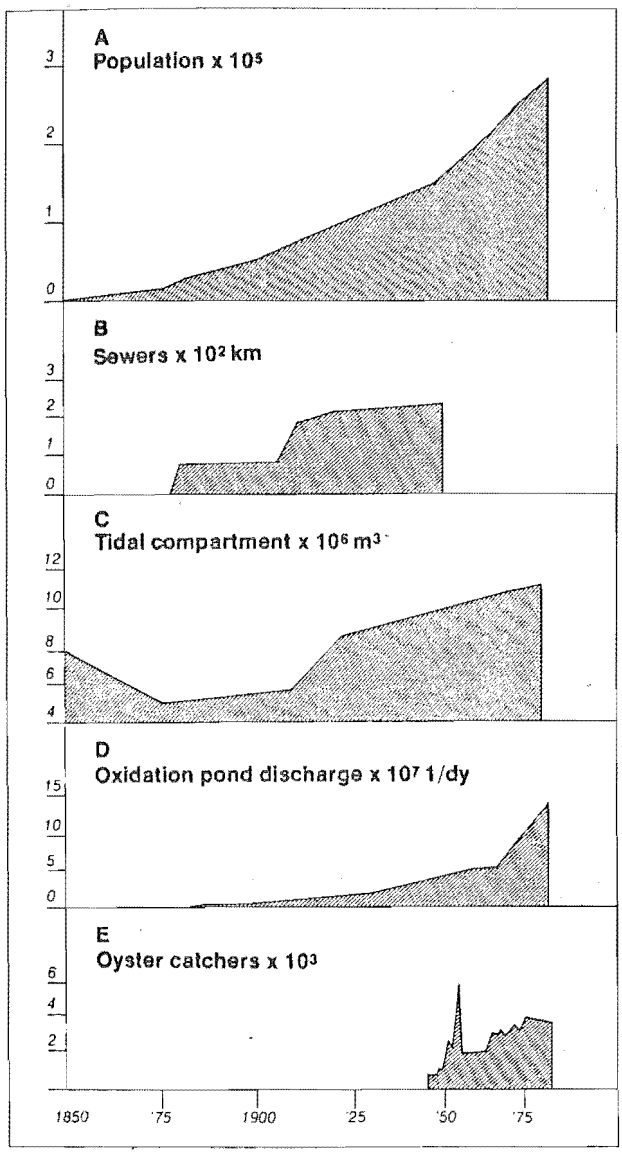

Fig. 1.4 Events in the Avon-Heathcote Estuary and its drainage basin: 1850-1980. (A) population of Christchurch, (B) length of sewers (km), (C) volume of the tidal compartment, (D) volume of effluent discharge from Bromley Oxidation Ponds, (E) winter resident numbers of the South Island pied oystercatcher.

In 1926, the sewage farm system was replaced by the two-stage system of the Bromley Sewage Purification Works. Primary treatment (including mechanically cleaned screens, grit removal by means of aerated tanks, primary sedimentation with scum collection, trickling

filters, anaerobic digestion of solids and lagooning of digested residues) was followed by secondary treatment (by biological oxidation) in a series of ponds before discharge into the estuary. After 1950, there was a gradual diversion of some industrial effluents into the city sewage system for treatment (Fig. 1.4D). Industrial sewers and pumping stations were built connecting industrial areas with the sewage works and in 1971, with the completion of the Woolston industrial sewer and Pumping Station No. 15, almost all industrial discharges into the Heathcote River ceased (J. Robb, pers. comm.).

The rapid urban growth and accompanying change in vegetation cover of early settlement appears to have resulted in an increase in sediment supply to the Avon and Heathcote Rivers. The sediment was deposited in the estuary as a 50-60 cm thick layer of distinctive mud, and resulted in a decrease in the tidal volume of the estuary by an estimated 30% between 1850 and 1875 (Fig. 1.4C; Macpherson, 1978).

It is reasonable to assume that this deposition of a thick layer of fine sediment over a short period of time would have altered the benthic invertebrate community immensely - and there is evidence that large mature populations of the bivalves *Chione stutchburyi* and *Mactra (Cyclomactra) ovata tristis* (Reeve, 1854) were killed by this deposition, for beds of shells in natural orientation have been noted (Stephenson, unpubl. data) in association with this layer.

After 1875, sediment yields were reduced, due to improvements in drainage of the city area and increased impervious cover (roofs and roads) which altered run-off characteristics. The estuary responded with an increased tidal compartment to a present volume which is slightly greater than that of 1850, and which appears to be approaching stability. The estuary remains a net exporter of sediment (Macpherson, 1978, in press a, b).

Encroachment of urban development on the rivers and estuary led to reclamation of a great deal of the bordering high tide wetlands. Main river channels leading into the estuary have been widened and straightened and most of the perimeter of the estuary is now sea wall, or has some form of shore protection. Most notably, McCormacks Bay was separated from the estuary by a causeway which severely restricted flow and changed the tidal regime and later was partially infilled.

The first biological study of the Avon-Heathcote Estuary was carried out in 1928-9 (Thompson, 1930). At this time a few changes which

had occurred in the fauna were evident. The bivalve *Mactra tristis* was represented by very few, small, living individuals, though large beds of shells of dead individuals were recorded. The whitebait *Galaxias attenuatus* which was "at one time common and bred in the estuary" had been severely reduced in number, and it was reported that "now only scattered individuals are taken". Shells of the cockle *Chione stutchburyi* were reported as being thin and fragile with an incidence of 60% infection by a burrowing polychaete worm. Although only a small amount of chemical analysis was undertaken as part of the 1928-9 survey, a marked decrease in dissolved oxygen concentration was apparent with increasing distance "upstream" in the estuary; especially toward the Heathcote River.

The report of a second survey undertaken in 1951 (Bruce, 1953) stated that "large areas of the mudflats about the main effluent, starch factory effluent and St Andrews Hill effluent, harbour a specialised fauna composed of only a few species. The restricted fauna in these areas indicate the presence of decaying organic matter derived from the effluents". The animal life in the rest of the estuary seemed unchanged from the earlier survey, although counts of the mud snail *Amphibola crenata* were greater. A significant change in flora of the estuary was apparent however. Blooms of the alga *Ulva lactuca* were apparent (whereas the earlier survey had referred to "... a little *Ulva* in sheltered rock pools and on muddy sand banks"), presumably in response to increased fertilisation.

These trends continued into the 1970s. Areas near the mouth of the Heathcote River and the oxidation pond outfall exhibited anaerobic conditions and a marked restriction in community diversity; and blooms of *Ulva* continued to develop. The Bromley Sewerage Works were by the early 1970s handling virtually all of the city effluent, including industrial wastes, and it was assessed in 1973 that the sewage works contributed 80% of the nitrogen and 94% of the phosphorus entering the estuary - far outweighing the natural load (Knox & Kilner, 1973).

The improved treatment and removal of all but the occasional (accidental or otherwise) discharge of industrial effluent into the Heathcote River has improved the state of the estuary. The high B.O.D. load of the Heathcote River (estimated in 1971 to be the equivalent of one-third of the B.O.D. of the Bromley oxidation ponds, released into 1.5 km of the river; J. Robb, pers. comm.) has been reduced. This, together with the practice of allowing discharge from the oxidation ponds

only on the outgoing tide (so that more of it goes out to sea rather than ponding around the outfall), has improved conditions around the effluent sites and has effectively reduced the nutrient load in the estuary. Whitebait *(Galaxias* spp.) have recently returned to catchable numbers and algal blooms have not been as severe in the last few years.

The estuary also has experienced the introduction of the cordgrass *Spartina* x *townsendii* (apparently to stop erosion near the Bridge Street bridge about the 1950s; Knox & Kilner, 1973) and there has been an astounding increase in numbers of the South Island Pied Oystercatchers *Haematopus ostralegus finschi* since 1950 (Fig. 1.4E) (Knox & Kilner, 1973). The latter event is not related to urbanisation of this particular drainage basin, but is associated with post-European settlement changes in New Zealand as a whole.

In addition to the changes mentioned, there have been others proposed at various times in the past which could have had serious effects on the estuary.

In the early 1900s a scheme to build a shipping canal linking Christchurch with the sea by way of the estuary was proposed. This plan called for a channel dredged to a depth of 30 ft (≃ 9 m) at spring low tide across the estuary and up the lower Heathcote River. Although seriously considered and hotly debated at the time, this scheme was abandoned in favour of improved port facilities and transportation to and from Lyttelton (Lyttelton Harbour Board, 1905, 1909a, 1909b; Little, 1911a, 1911b).

In 1917 the use of 300 acres of mud flat for a salt works was proposed but not carried out (J.B. Bushell, pers. comm.).

A problem of flooding during times of prolonged heavy rainfall, especially at spring tides, prompted consideration of flood relief schemes. In 1959 it was recommended that low water channels be dredged, McCormacks Bay be filled, and a barrier be constructed at the mouth of the estuary to control the tide. Hydraulic model tests of these and other schemes were carried out at the Hydraulics Research Station, Wallingford, England and reports (No. EX509) made in 1970 and 1972 supplied details of depth of channels and sizes of gates required. For a variety of reasons (technical, economic and environmental) these recommendations have not been implemented.

The Avon-Heathcote Estuary is unique amongst New Zealand estuaries in having had biological investigations carried out as early as 1928-9.

These have established a base line against which the numerous more recent studies could be compared. Most significant in terms of estuary management was the completion in 1973 of a comprehensive report *The Ecology of the Avon-Heathcote Estuary* (Knox & Kilner, 1973; prepared for the Christchurch Drainage Board by the Estuarine Research Unit, Department of Zoology, University of Canterbury) which not only assessed the biological, physical and chemical state of the estuary but established goals and objectives for future management. The overall management objective was defined as "the achievement of the best combination of uses to serve the needs of society while protecting, preserving and enhancing the biophysical environment for the continued benefit of present and future generations", and specific goals and recommendations (including drastic moderation of the proposed flood relief scheme and the recommendation that a few areas be set aside as reserves) were made toward this objective (see also Appendix 1).

1.2.3 The Application of Energetics to the Study of Estuaries

The study of ecological energetics of multiple species systems, a field pioneered by Lindeman (1942), has focussed primarily on aquatic communities (Wiegert, 1976). Notable are the early studies of a coral reef by H.T. Odum & E.P. Odum (1955) and investigations of Silver and Root Springs by H.T. Odum (1957) and Teal (1957) respectively.

The aquatic system, and especially spring ecosystems, offered general advantages for this type of study including ease of delineation of system boundaries, and a relatively low total number of species to consider; and Wiegert (1976) pointed out that there was no comparable energy flow study of a terrestrial ecosystem almost two decades later.

The impetus for pursuing multiple species energy flow studies has been the contention (demonstrated for example in the study of E.P. Odum & Smalley (1959) comparing an herbivore and a deposit feeder, and in the terrestrial food chain study of Golley (1960)) that this provides a way of analysing and understanding the organisation and function of an ecosystem (Wiegert, 1976).

The multiple species energy flow approach was applied to a more complex salt-marsh community by Teal (1962), and that energy flow diagram, although based upon a great number of assumptions and gross generalisations, allowed insight into the magnitude of energy terms (for example, the high

proportion of *Spartina* production that is lost to respiration (70%), and the estimated export of marsh production (45%) to an estuary).

The overall state of an ecosystem is dependent upon, and may be investigated in terms of, the flow of energy through the system. Such an investigation allows an ecological understanding of a system; and the generation of data may allow creation of a model for prediction of changes in its state, and a greater understanding of biological components and the flow of energy within and between these components.

Estuaries traditionally have been preferred sites of human settlement, as they meet needs such as transportation, harbour, effluent disposal and food availability. Not only are they subject to intensive use in their own right, but they receive the impact of activities throughout the entire watershed. As estuaries form the apex of land drainage systems; they reflect the state of the drainage basin and are sensitive to changes within the watershed.

Estuaries and enclosed embayments lend themselves particularly well to whole ecosystem studies for the same reasons presented by Mann (1975) for enclosed seas:

(1) boundary conditions are usually well defined,

(2) nutrient, salt and water budgets can often be framed with more precision than elsewhere,

(3) small basins lend themselves to whole-system field experiments, and

(4) from a practical viewpoint, these areas often serve as waste sinks and give rise to serious management problems; such as conflict of interest between waste disposal and recreation or aquaculture.

It is not surprising in view of these features that a variety of estuarine and coastal systems have been the subject of studies in community energetics (for example, Teal, 1962; Golley *et al.*, 1962; Mann, 1969; W. Odum, 1971; Pamatmat, 1968; Day *et al.*, 1973 etc.) and have featured prominently in the development of the field of ecosystem modelling (Nihoul, 1975; Kremer & Nixon, 1978; Dame, 1979; section 5.1).

The Avon-Heathcote Estuary offered an excellent system in which to conduct a study of energetics for the following reasons:

(1) well defined estuary and drainage basin,

(2) size suitable for thorough spatial sampling,

(3) wealth of background knowledge and data base (including the biological aspects),

(4) ease of access, and

(5) concern for effective management and interest in the effect of urbanisation of the drainage basin.

The importance of the intertidal mudflat community - a very extensive and typical feature of many estuaries - has been stressed in several studies, but few attempts have been made to quantify it (Warwick & Price, 1975).

Study of the energetics of single estuarine species have been aimed at this and while several studies of the metabolism of benthic communities have demonstrated that macrofauna play a minor role in total energy flux (Carey, 1967; Pamatmat, 1968; Smith, 1973), Bahr (1976) demonstrated that communities of high biomass such as oyster reefs may be significant.

More often, production values for macrofaunal communities have not been compared with total system production to assess significance (e.g. Warwick & Price, 1975; Wolff & de Wolf, 1977; Warwick *et al.*, 1978).

In this study, the role of one species in the energy flow of a particular estuary will be defined and quantified by comparison with energy flow through the entire system. It is also hoped that the results will have wider application, to further defining the role of benthic communities in general in the energy flow of estuarine systems.

1.3 THE COCKLE *CHIONE (AUSTROVENUS) STUTCHBURYI* (WOOD, 1828)

1.3.1 Nomenclature

Nomenclature of the New Zealand cockle (Maori: huangi or tuangi (Powell, 1976)) has had an interesting and confused history. It is a venerid bivalve referred to by the most recent local authority (Powell, 1979) as *Chione (Austrovenus) stutchburyi*. It occurs in the North, South, Stewart and Chatham Islands while a second species *C. (A.) aucklandica* is found at the Auckland Islands.

Genus CHIONE Megerle, 1811
Subgenus AUSTROVENUS Finlay, 1927

Type (OD) *Venus stutchburyi* Gray = Wood, 1828

Shell similar to *Chione cancellata* (Linnaeus, 1767), but more orbicular and inflated, with the radial sculpture dominant over the concentric lamellae, and the escutcheon scarcely apparent. New Zealand, Waitotaran middle Pliocene to Recent.

Chione (Austrovenus) stutchburyi (Wood, 1828)
Plate 77:11

North, South, Stewart and Chatham Islands, very common on tidal mud and sand flats. The edible so-called cockle of New Zealand.

Shell large, solid, rotund and considerably inflated, sculptured with numerous strong rounded radial ribs, overridden by crisp weak lamellae. Colour whitish, tinged at the posterior end, with pale purplish-brown; internally whitish, stained posteriorly with dark purplish-violet. Northern shells tend to be globose and inflated, southern shells obliquely ovate and less inflated.

Height 47.0–56.0 mm., length 51.0–62.0 mm., thickness 39.0–42.0 mm.

Venus stutchburii Wood, 1828, suppl. pl. 2, *Venus*, fig. 4. *Chione stutchburyi* (emended), Hutton, 1873, p. 70. Suter, 1913, p. 987. *Austrovenus*, Finlay, 1927A, p. 470. Marwick, 1927, p. 620.

Chione (Austrovenus) aucklandica Powell, 1932
Plate 77:10

Auckland Islands (type), common at Carnley and Laurie Harbours, on tidal mud flats.

The Auckland Islands species is ovate-quadrate, and less inflated than any of the forms of *stutchburyi*. It also differs in sculpture, the radials being more numerous, and without concentric lamellae, other than irregular growth lines. Colour, externally chocolate-brown, and internally creamy-white, with or without posterior and ventral violet staining.

Height 51.0–53.5 mm., length 62.0–63.5 mm., thickness 33.0–35.0 mm.

Chione (Austrovenus) aucklandica Powell, 1932A, p. 68

(Powell, 1979: 426)

Confusion exists in the literature over the authority for the specific name (Gray, 1828 or Wood, 1828) (see for example Fischer-Piette & Vukadinovic, 1977; Powell, 1976, 1979). It appears that "*stutchburii*" is a manuscript name of Gray and was first published by Wood (1828) who also figured a specimen in the British Museum (Wilkins, 1955; B.A. Foster, pers. comm. - Appendix II).

In the most recent revision of the sub-family Chioninae (Fischer-Piette & Vukadinovic, 1977: 94) *"Austrovenus"* is recognised as a genus, and the nomenclatural bibliography they give is reproduced below:

97. — AUSTROVENUS STUTCHBURII Gray

Venus stutchburii, Gray *in* Wood, 1828*b*, suppl. : 58, pl. 2, fig. 4.
Venus zelandica, Quoy et Gaimard, 1834, III : 522, pl. 84, fig. 5, 6.
Venus stutchburii Gray, Gray, 1835 (épreuve d'imprimerie au British Museum) ; Hanley, 1843 : 117 ; Gray *in* Dieffenbach, 1843, II : 250 ; Sowerby, 1853, II : 713, pl. CLV, fig. 50, 51 ; Reeve, 1863, XIV, pl. XV, fig. 59.
Venus zeilanica Quoy, Deshayes, 1835, éd. 2, VI : 373.
Venus zelanica Quoy, Hanley, 1843 : 127.
Venus dieffenbachii, Gray *in* Dieffenbach, 1843, II : 250.
Venus zelandica Q. et G., Gray *in* Dieffenbach, 1843, II : 250.
Venericardia zelandica, Potiez et Michaud, 1844, II : 166.
Chione stutchburyi Gray, Deshayes, 1853*a* : 137 ; Römer, 1867*b* : 108 ; Hutton, 1878, 26 : 49 ; Hutton, 1904 : 89 ; Suter, 1909, I : 46 ; Suter, 1913 : 987, pl. 61, fig. 4 ; Graham, 1962, II (9 : 56 ; Powell, 1962 : 123, pl. 15, fig. 2.
Venus zealandica Gray, Hutton, 1873 : 69.
Chione stuchuryi Gray, Hutton, 1873 : 70.
Chione dieffenbachi Gray, Hutton, 1873 : 70.
Venus (Chione) stutchburyi Gray *in* Wood, Martens, 1873 : 45.
Venus (?) dieffenbachii Gray, Martens, 1873 : 45.
Venus (Chione) stutchburii Gray, Smith, 1874, *Zool.*, II, *Moll.* : 6, pl. 3, fig. 4.
Venus (Chione) stutchuryi Gray, Tenison-Woods, 1878 : 51.
Venus (Chione) macleayana, Tenison-Woods, 1878 : 51.
Chione stuchburyi Gray, Hutton, 1880 : 148.
Venus stutchburyi Gray *in* Wood, Hutton, 1885, IX (1884) : 522.
Chione macleayana Ten.-Woods, Tate et May, 1901, XXVI : 427.
Chione stutchbury Gray, Suter, 1906, XXXIX : 269.
Venus zealandica Q. et G., Hedley, 1916*a*, I : 166.
Venericardia zelandica Pot. et Mich., Lamy, 1921, 66 : 303.
Austrovenus stutchburyi Gray, Finlay, 1927, LVII : 470 ; Finlay, 1928, LIX : 278.
Venus (Chione) stutchburyi Wood, David, 1933, Bd. 15, nº 1-6 : 132.
Chione (Austrovenus) stutchburyi Gray, Powell, 1939, II (4) : 213.
Venus zelandica Q. et G. = *Chione stutchburyi* Gray, Fischer-Piette et Lamy, 1942 : 130.
Chione stutchburyi, Paul, 1966, IX (1) : 30 ; Hyde, 1967, 10 (3) : 723 ; Penniket, 1970 : 94, pl. 44, fig. 2.
Chione stutchburii Wood, Dance, 1971, XXVI (6) : 376.

(Fischer-Piette & Vukadinovic, 1977: 94)

Finlay (1927) introduced the generic name *Austrovenus* without adequately describing the entity to which it referred or linking the new generic name properly with *"stutchburyi"*.

Marwick (1927) later in the same volume placed *"Austrovenus* Finlay, 1927" as a subgenus within *Chione*, but his paper is not cited by Fischer-

Piette & Vukadinovic (1977) - a serious omission in that it provides the most detailed account of the species:

8. Genus CHIONE, Megerle 1811.

Type: *Venus cancellata* Linné.

a. Subgenus Austrovenus Finlay, 1927.

Type: *Venus stutchburyi* Gray.

Shell fairly large, oval. Lunule large, not impressed, radially ribbed, bounded by shallow depression not by incised line; escutcheon defined by absence of radials, shallow on flat specimens but fairly deep on thick inflated ones. Sculpture of rounded radial ribs, with narower interstices crossed by low, well-spaced, irregular, concentric lamellae which often die out on posterior half of shell, posterior area marked by obsolescence of radials. Hinge-teeth all divergent; left valve with long, high, curved, posterior cardinal welded to nymph; broadly-triangular, slightly-curved, grooved median; and strong, triangular, often obscurely-grooved, anterior one. Right valve with long, somewhat narrow, curved, grooved posterior cardinal; short, broadly-triangular, grooved median, and narrow lamellar anterior one. Pallial sinus short, ascending. Pedal retractor close to and often joining adductor. Valve-margins bicrenate.

Austrovenus is closely related to *Chione* s. str. as shown by the close agreement of the hinge, pallial sinus, marginal crenation and sculpture. The Recent *C. stutchburyi* differs principally from *C. cancellata* in lacking the well-defined concave escutcheon which imparts a triangular shape, and in the concentric lamellae being less persistent and lower. The Californian *Chione fluctifraga* Sowerby also is without a concave escutcheon and so agrees closely with *A. stutchburyi* in shape and general characters. The sculpture, however, differs, for the concentric ribs are flattened out and have smooth surfaces. Fossil ancestors of *C. stutchburyi* from the Pliocene have an escutcheon almost as well defined as that of *C. cancellata*. *Chione* seems to be regarded by some authors as preoccupied by the prior *Chion*, but as one is the name of a goddess and the other that of a man this course does not seem justified. The words themselves are not synonymous.

Chione (Austrovenus) stutchburyi (Gray). (Figs. 158-60.)

1927 *Austrovenus stutchburyi* (Gray): Finlay (this volume).

For synonymy see *Chione stutchburyi* Suter's *Manual*, p. 987.

Suter said that the escutcheon " is wanting," but this is not correct. It is marked by the absence of radial ribs and in large, heavy individuals it is quite deeply sunken.

Localities: Recent (type): 1102, Waipaoa beds, Awatere River, East Cape; Castlecliff; Kai-iwi; Okehu; Nukumaru; Marae-kakaho.

(Marwick, 1927: 620)

and states that it compares well with *Chione* s. str. as shown by "close agreement of the hinge, pallial sinus, marginal crenulation and sculpture".

From the literature it is very hard to support the case for separate generic status of *Austrovenus* especially when based upon shell morphology alone.

The description of *Chione (chione* s. str.) given by Fischer-Piette & Vukadinovic (1977: 6) translates as follows:

> In this subgenus the sculpture is cancellate with concentric ribs more marked than radial ribs but without projections at the intersections. The number of radial ribs increases with age but without bifurcation. The lunule and the ligament area are well delimited. The median cardinal tooth of the right valve is very large at its base and its relief attenuates from the sommet to the base (where it is by no means projecting). The pallial sinus is very short with an angle to the sommet very open.

Their description of *Austrovenus* (pp. 94, 95) is as follows:

> The sculpture varies from one region of the shell surface to another. In the median (central) part the sculpture is decussate (criss-cross, x-shaped) in the region of the sommet (peak or vertex) and further, in at least one part of this region the radial lines are on top of the concentric lines whose slightly elevated lamellae are made sinuous by the crossing of the radial lines. In the anterior region, the concentric lines are very elevated (distinct), they prevail over the radial lines which are by contrast attenuated, and at the points of crossing they do not cause the sinuous pattern of the concentric rings. In the posterior region, the sculpture is considerably attenuated: near the posterior edge, one cannot distinguish more than light growth lines, crossed by light radial lines which are barely perceptible. The ligament is very prominent.

Jones (1979) presented the first thorough anatomical consideration of the soft parts of members of the group of venerids to which *stutchburyi* belongs (*C. cancellata, C. undatella, C. paphia, Mercenaria mercenaria* and *Austrovenus stutchburyi*) and concluded that *A. stutchburyi* "although superficially similar to the cancellate American chionines, differs from them in complex characters, and is probably not closely related to them". "In some characters it resembles *Mercenaria*, but in many conchological characters it resembles equally well *Protothaca* and some members of the Tapetinae. The differences of anatomy, particularly the stomach, dentition, and siphons, and the lack of fossil intermediates indicate that *Austrovenus* does not belong to the Chioninae. It seems more likely that the similarity of *Austrovenus* to *Chione* in sculpture is the result of convergent evolution of very different lineages adapting to a shallow infaunal mode of life in shifting substrata in the intertidal and shallow subtidal zones".

There are, however, observations which make the separation less clear:

(1) shell morphology, growth and condition of *C. stutchburyi* are extremely variable throughout New Zealand (Larcombe, 1971), and even within one estuary (this study) (the individuals dissected by Jones (1979) came from one site near Auckland),

(2) a few young (10-20 mm) individuals of *C. stutchburyi* have been noted to have commarginal lamellae forming broad ridges at their posterior ends, typical of *Chione* s. str. (Stephenson, unpubl. data), and

(3) larval characteristics of *C. stutchburyi* are very similar to those of *C. cancellata* (see section 1.3.3).

Fischer-Piette & Vukadinovic (1977: 96) cast doubt on the separation of *C. stutchburyi* and *C. aucklandica* as follows:

> The species *C. aucklandica* is certainly very near *C. stutchburyi* and it would be desirable to be able to check the justification for the separation, given the remarkable variability that is present in *stutchburii* from all points of view: general form, degree of lengthening (plasticity), degree of distention (enlargement), position of the sonnetts, development and attenuation of the sculpture, degree of predominance of the radial or concentric sculpture; shape, form, clarity, dimensions of the lunule; shape, clarity, degree of lengthening of the ligament, crenulations of the lower edge of the valves; form and dimensions of the cardinal tooth and variability of the other teeth; colour of the exterior and interior, etc. This variability is evident in each of the 58 specimens of our collections.

There is a case for further investigation of this distinction.

In this thesis, the nomenclature of Powell (1979) is followed, although the anatomical evidence of Jones (1979) that *C. stutchburyi* is slightly different from *Chione* in the strict sense is acknowledged.

The distribution of *C. stutchburyi* is reported by Fischer-Piette & Vukodinovic (1977: 96) as follows:

> "According to the literature, this species is known from New Zealand (a number of authors), Chatham Island and the Auckland Islands (Hutton, 1878, 1880), the Kermadec Islands (Suter, 1913), Tasmania (Tenison-Woods, 1878), Bass Strait (Tate & May, 1901), South West Australia (Martens, 1873), Kerguelen (Deshayes, 1853), somewhere in the Sandwich archepelago (Hanley, 1843, repeated in Reeve, 1863). In addition, Quoy & Gaimard cite the Port of King George in Western Australia, but Hedley (1916) considers this to be an error. We have a certain number of specimens from New Zealand (several donors), Stewart (Filhol, 1875) and from Melbourne (Muller, 1864)."

It appears that records from places other than New Zealand, the Chatham Islands and the Auckland Islands are erroneous (Powell, 1979; W.F. Ponder, pers. comm.).

1.3.2 Previous Studies

C. stutchburyi is known as a fossil from the Waitotaran middle Pliocene to Recent (less than 2-7 million years BP) (Gregg, 1959; Grant-Taylor & Beu, 1974; Powell, 1979; Fleming, 1979). It has also been noted extensively in sub-fossil deposits and archeological investigations (e.g. Trotter, 1975).

C. stutchburyi is a very common member of the fauna of New Zealand estuaries and protected harbours (Morton & Miller, 1973; see section 2) and studies have been reported of its growth characteristics (Coutts, 1974), larval development (Stephenson & Chanley, 1979; see section 1.3.3), general distribution and community association (Wood, 1962; Rainer, 1969; Knox & Kilner, 1973; Knight, 1974; Voice, 1975; Estcourt, 1976; Stanton *et al.*, 1977; Grange, 1977; Richardson *et al.*, 1979; Healy, 1980).

The most extensive investigation of the ecology of *C. stutchburyi* is that of Larcombe (1971) in which population dynamics and some estimated energy parameters of populations from Auckland, Wellington, Christchurch and Dunedin are compared.

The need for research into aspects of the ecology of *C. stutchburyi* is increasing, for the cockle is the basis of a popular recreational fishery (Watkinson & Smith, 1972) and has recently become part of the commercial shellfishery of New Zealand (yield 50,600 kg in 1979 - A.R. Branson, pers. comm.; Appendix III). In addition, as an animal with wide distribution in areas of increasing environmental awareness and concern (especially estuaries), research into its ecology, especially preferences and tolerances, is valuable and should enable its use as an indicator species to be assessed.

1.3.3 Larval Development of *C. stutchburyi* Reared in the Laboratory

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Larval development of the cockle *Chione stutchburyi* (Bivalvia: Veneridae) reared in the laboratory

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Larvae of the New Zealand cockle *Chione stutchburyi* (Wood, 1828) reared to settlement in the laboratory are described. They are characterised by dissimilar shoulders with a large, broadly rounded anterior shoulder and end, and broadly rounded umbo, typical of the Veneridae. Setting occurred after 20 days at a minimum length of 180 μm. Shell dimensions increased linearly during larval development but hinge length did not. The L:H ratio decreased from 1.27 at L = 100 to 1.1 at L = 200 and the L:D ratio from 1.95 at L = 100 to 1.59 at L = 200. An SEM study revealed that the larval hinge is characterised by a toothed provinculum forming a broad medial projection on the right valve, opposing two projections on the left valve. Conspicuous flanges on the anterior and posterior shoulders of the left valve fit into corresponding grooves of the right valve.

INTRODUCTION

The cockle *Chione stutchburyi* (Wood, 1828)* is a common member of New Zealand estuarine faunas, yet little has been published of its general ecology. It occurs in lower intertidal mud/sand flats of protected estuarine areas throughout New Zealand (Morton & Miller 1973, Powell 1976, Grange 1977, Stanton *et al.* 1977, Stephenson 1978), often dominating such areas with population densities up to 3000/m². Maximum age and growth rate are extremely variable, but populations 20 years old and reaching shell lengths greater than 60 mm have been recorded (Stephenson, unpubl. data). Sexes are separate, and gonadal development (in individuals larger than 18–20 mm shell length) peaks in January, spawning taking place over a protracted late summer season in populations from Auckland to Dunedin (Larcombe 1971).

This species is not part of the commercial shell fishery at present, but it does sustain a popular recreational fishery (Watkinson & Smith 1972).

The purpose of this paper is to describe the larval development of *C. stutchburyi* in the laboratory, with a view to facilitating its identification in the plankton and hence assessment of spatfall. To this end, the general development and dimensions of the larval shell (as in Chanley & van Engel 1969, Chanley & Andrews 1971) and an SEM study of the hinge structure are described.

Although this is the first description of a New Zealand veneracean larva, it joins comparable descriptions of species of Ostreacea (Dinamani 1973, 1976, Booth 1979a), Mytilacea (Booth 1977), Pteriacea and Anomiacea (Booth 1979a), and Leptonacea (Booth 1979b).

MATERIALS AND METHODS

Adult *Chione stutchburyi* were collected from the intertidal flats at Petone Beach, Wellington Harbour (41°14'S, 174°53'E), by staff members of the Fisheries Research Division's Mahanga Bay Shellfish Hatchery and maintained in the hatchery at approximately the salinity of the natural habitat (33‰).

Repeated attempts to induce spawning in animals collected periodically from September 1977 to February 1978 failed. Methods included temperature fluctuation by as much as 20°C (from ambient temperatures of 10–14°C to 28–30°C), addition of stripped sperm to the water, addition of algal food, and combinations of these. However, in February 1978 larvae were obtained by stripping the gonads, treating the eggs with ammonium hydroxide, and

*Fischer-Piette & Vukadinovic (1977) refer to this species as *Austrovenus stutchburii* (Gray). The reasons for this reclassification are unclear, and the nomenclature of Powell (1976) is followed here.

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artificially inducing fertilisation. Eggs treated with a 0.3% solution of 1N NH_4OH for 20 min to dissolve the germinal vesicles (Loosanoff & Davis 1963, D'Asaro 1967) produced a 12% yield of normal larvae. Far fewer larvae developed from eggs treated with a 1.2% solution of 1N NH_4OH or a 3% solution of 0.1N KOH, and there was no development in those treated with 3% solutions of 1N NH_4OH or 0.1N NaOH, or in untreated eggs.

Larvae were reared in 70-litre cylindrical polyethylene containers at an average temperature of 25.5°C (range 23–31°C) in sea water which had been filtered through diatomaceous earth and 1 μm candle filters. Water was changed daily by draining through a nylon screen of 35 μm mesh diameter. Larvae that were not in suspension when the water was changed were assumed to be unhealthy, and were discarded.

Larvae were maintained on a diet of the algae *Tetraselmis suecica*, *Pavlova lutheri*, *Isochrysis galbana*, and *Chaetoceros calcitrans*. Digestive diverticulum colour was observed daily to assess the value of the diet, and the algal rations were adjusted accordingly.

Periodically, subsamples of the larval culture were removed and the animals were fixed in a solution of 5% formalin + 10% sugar + 15% TRIS, then preserved in a solution of 10% propylene glycol + 1% propylene phenoxytol + 5% formalin (Turner 1976) buffered to pH8 with sodium glycerophosphate.

Maximum anterior–posterior length, maximum dorsal–ventral height, anterior end, posterior end, anterior shoulder, posterior shoulder, and umbo height (see Fig. 1) were measured on 130 larvae over the full range of sizes and developmental stages at ×125 magnification with a calibrated graticule micrometer eyepiece. On straight hinge stage individuals, hinge length was measured also. Because of the difficulty of manipulating larvae under the microscope, depth could not be measured on all individuals, so length and depth were measured on an additional 130 individuals to derive an L:D relationship.

Shell valves were prepared for scanning electron microscopy as follows. Larvae were washed in a 25% solution of chloronal bleach ('Janola') in distilled water for 15 min to separate shell valves and remove tissue, rinsed four times in distilled water, and dehydrated through an aqueous acetone series (10, 25, 50, 75, and 100% acetone), 10–15 min at each dilution. Individual valves were then dropped on to double-sided Sellotape and dried over a desiccant. Samples were gold-coated to a thickness of 3500 nm using a Poleron E55 Diode Sputterer and examined in a Cambridge Stereoscan 600.

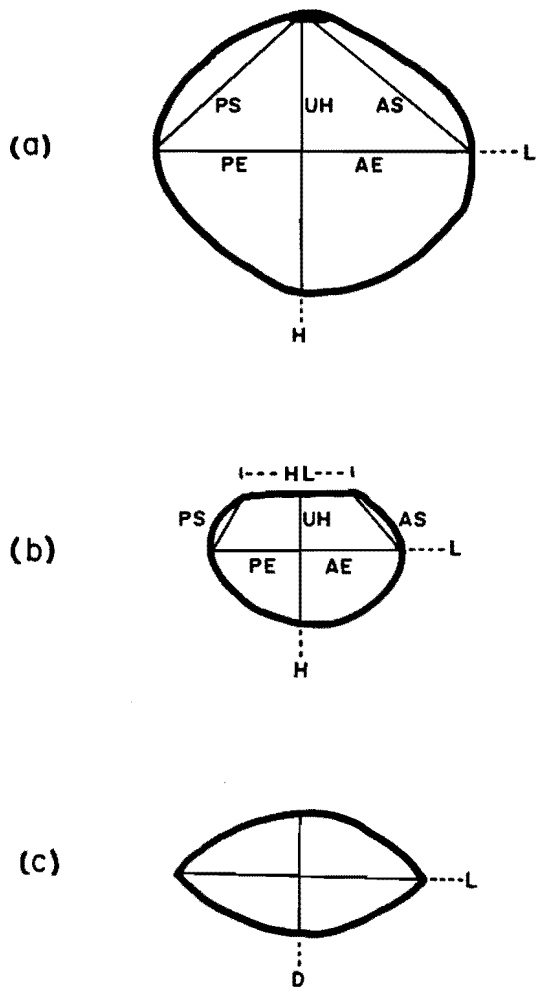

Fig. 1. Measurements used to describe the dimensions of larval *Chione stutchburyi*: length (L), height (H), depth (D), anterior end (AE), posterior end (PE), anterior shoulder (AS), posterior shoulder (PS), umbo height (UH), and hinge length (HL). (**a**), (**b**), lateral views of umbonate and straight hinge stages; (**c**), dorsal view.

RESULTS

Development

Photomicrographs of larvae at a series of sizes are presented in Fig. 2.

Typical straight hinge veligers were present within 48 h of fertilisation (at 25°C). At this stage the anterior shoulder and anterior end are larger and more rounded than the posterior, and an apical flagellum at least 50 μm long is present. During the straight hinge was 61.6±1.7 μm (range 51–71 μm), μm, and D = 48–70 μm. The mean length of the straight hinge was 61.6+1.7 μm (range 51–71 μm),

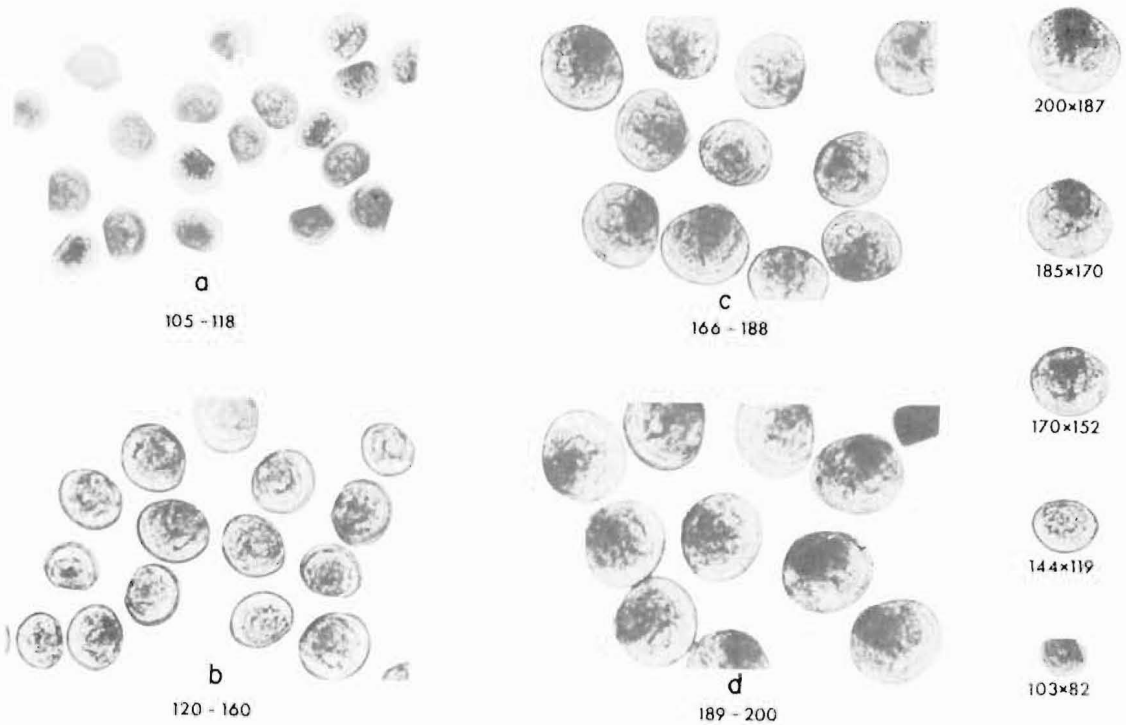

Fig. 2. Photomicrographs of *Chione stutchburyi* larvae. Representative individuals (*right*) are arranged with the anterior end to the right (length × height in μm). (**a**), 1-day-old straight hinge larvae; (**b**), (**c**), early and well developed umbonate larvae; (**d**), late umbonate larvae just before setting (length range in μm).

and hinge length did not increase with increasing total body length.

The umbonate stage appeared when L was between 116 μm and 139 μm. The umbo is broadly rounded, and the shoulders are dissimilar (the anterior shoulder is much longer than the posterior), a shape that is typical of venerid larvae (La Barbera & Chanley 1970, Le Pennec 1973). During the umbonate stage L = 116–215 μm, H = 90–117 μm, and D = 58–128 μm.

A non-functional foot was first noted at length 165 μm, and a pediveliger with a functional foot at L = 175 μm. Setting juveniles with gills and a foot but no velum appeared at L = 180 μm; the largest individual noted with a functional velum was 215 μm long. During the pediveliger stage L = 175–215 μm, H = 158–197 μm, and D = 105–130 μm.

Larvae first set approximately 20 days after fertilisation, on the bottom of the culture chamber, i.e., with no additional substrate. Mean daily measurements indicated that the growth rate fluctuated markedly, and was very slow when diet was inappropriate (as reflected by pale digestive diverticulum colour). Development was slower than in other venerid larvae (Chanley, unpubl. data), but would probably have been more rapid had larvae fed consistently.

Table 1. Regression equations and product-moment correlation coefficients of total length of larval *Chione stutchburyi* on height, depth, umbo height, anterior shoulder, posterior shoulder, anterior end, and posterior end (see Fig. 1).

				r
H	=	1.04L	− 25.14	0.99
D	=	0.78L	− 22.57	0.92
UH	=	0.58L	− 23.14	0.96
AS	=	0.99L	− 52.31	0.92
PS	=	0.86L	− 49.65	0.91
AE	=	0.66L	− 13.17	0.98
PE	=	0.34L	+ 12.73	0.92

Dimensions

Regression of total length on other body parameters (using Bartlett's three-group model II regression technique; Simpson *et al.* 1960) indicated that shell dimensions increase linearly during the larval phase (Table 1). Variation in depth and height are plotted against length in Fig. 3 in the way suggested by Chanley & van Engel (1969).

According to the regression equations (Table 1),

the L:H ratio decreases from 1.27 at L = 100 to 1.1 at L = 200, and the L:D ratio from 1.95 at L = 100 to 1.59 at L = 200.

SHELL MORPHOLOGY AND HINGE STRUCTURE

The external shell of larval *C. stutchburyi* has the smooth, D-shaped structure of prodissoconch I surrounded by the fine striae of the prodissoconch II shell, as noted in other venerids (Carriker 1961, Chanley & Andrews 1971). The prodissoconch I shell is also defined in most larvae by a ridge inside the valve.

A schematic view of the umbonal area is presented in Fig. 4. A straight provinculum bearing numerous small teeth on each valve remains in contact when the valves are gaping. Anteriorly and posteriorly the lateral hinge structure is characterised by flanges on both the anterior and posterior shoulders of the left valve which fit into grooves of the right valve (Fig 5a, b). A prominent ridge marks the ventral margin of the anterior right valve groove and extends posteriorly to a solid lateral tooth (Fig. 5b). The provinculum of the left valve has two toothed projections, one anteriorly (Fig. 5d) and a smaller one posteriorly (Fig. 5c). These leave a medial gap (Fig. 5c), corresponding to a medial

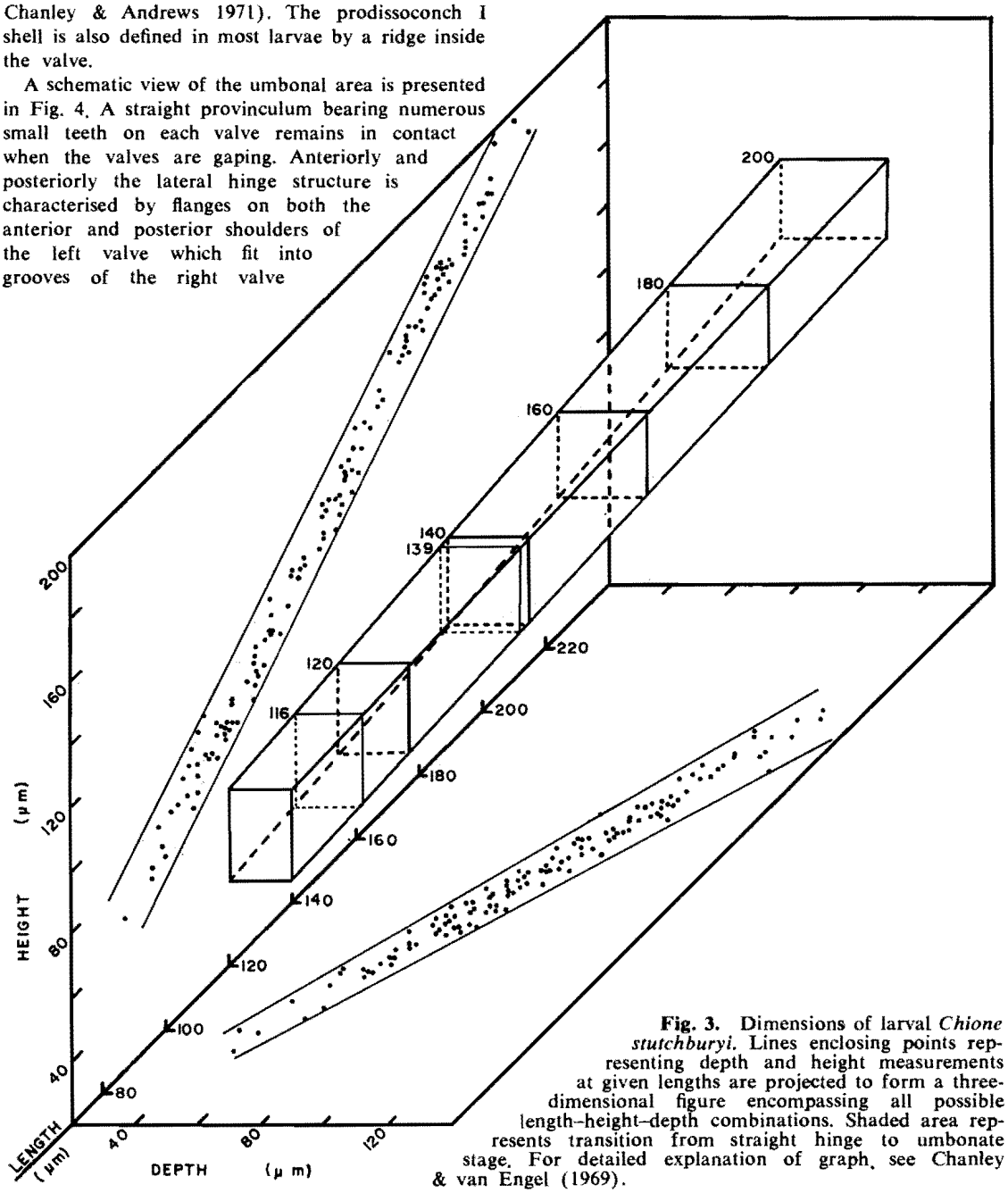

Fig. 3. Dimensions of larval *Chione stutchburyi*. Lines enclosing points representing depth and height measurements at given lengths are projected to form a three-dimensional figure encompassing all possible length–height–depth combinations. Shaded area represents transition from straight hinge to umbonate stage. For detailed explanation of graph, see Chanley & van Engel (1969).

series of teeth on the provinculum of the right valve (Fig. 5e). The anterior tooth of the left provinculum opposes the solid lateral tooth of the right valve on closure (Fig. 5b, d).

Rees (1950) described 18 basic types of lamellibranch larval hinge, 14 of which correspond to single superfamilies. The hinge of larval *C. stutchburyi* appears very similar to the "venerid type c" hinge illustrated by Rees (1950) – rough projections on the provinculum, prominent ridges on the lateral hinge system, and a long anterior tooth of the left provinculum opposing a solid lateral tooth of the right valve on closure. Smaller larvae have reduced major projections of the provinculum and small, interlocking provincular teeth (Fig. 5f, g).

DISCUSSION AND CONCLUSIONS

Temperature fluctuation has been used successfully to induce spawning of *Venus striatula*, *V. verrucosa*, *V. fasciata*, *Venerupis pullastra*, and *V. aurea* (Le Pennec 1973), *Tapes semidecussata* and *Mercenaria* species (Loosanoff & Davis 1963, Bardach *et al.* 1972), and *Chione cancellata* (La Barbera & Chanley 1970). It has not been found effective, however, in *Pitar morrhuana* (Loosanoff & Davis 1963), *Chione cancellata* (D'Asaro 1967), *Chione stutchburyi* (this study), and many other venerids (Chanley, unpubl. data).

Treatment of stripped eggs with a 0.3% solution of 1N NH_4OH appears to be a successful culture technique (Loosanoff & Davis 1963, D'Asaro 1967).

C. stutchburyi has a 4-month spawning period, from January to April (Larcombe 1971; Stephenson, unpubl. data). Assuming a natural development time similar to that observed in culture, of about 20 days, spatfall would be expected to occur from February to May.

The shape and dimensions noted in this study for *C. stutchburyi* are very similar to those reported for *C. cancellata* reared in North Carolina (La Barbera & Chanley 1970) and for *C. ulocyma* from Miocene deposits of Florida (La Barbera 1974). The excellent account of the internal development and anatomy of *C. cancellata* presented by D'Asaro

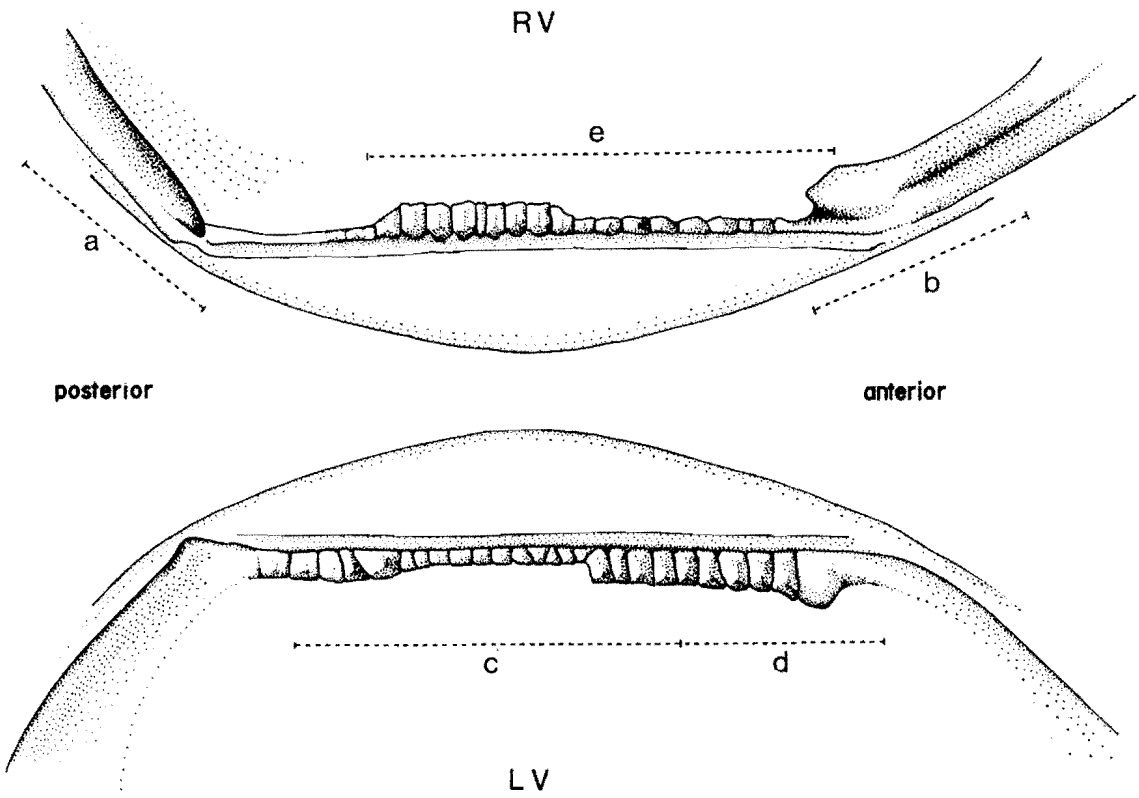

Fig. 4. Hinge structure of left *(below)* and right *(above)* valves of late stage (185–200 μm) larval *Chione stutchburyi*. Letters denote areas shown in Fig. 5a–e.

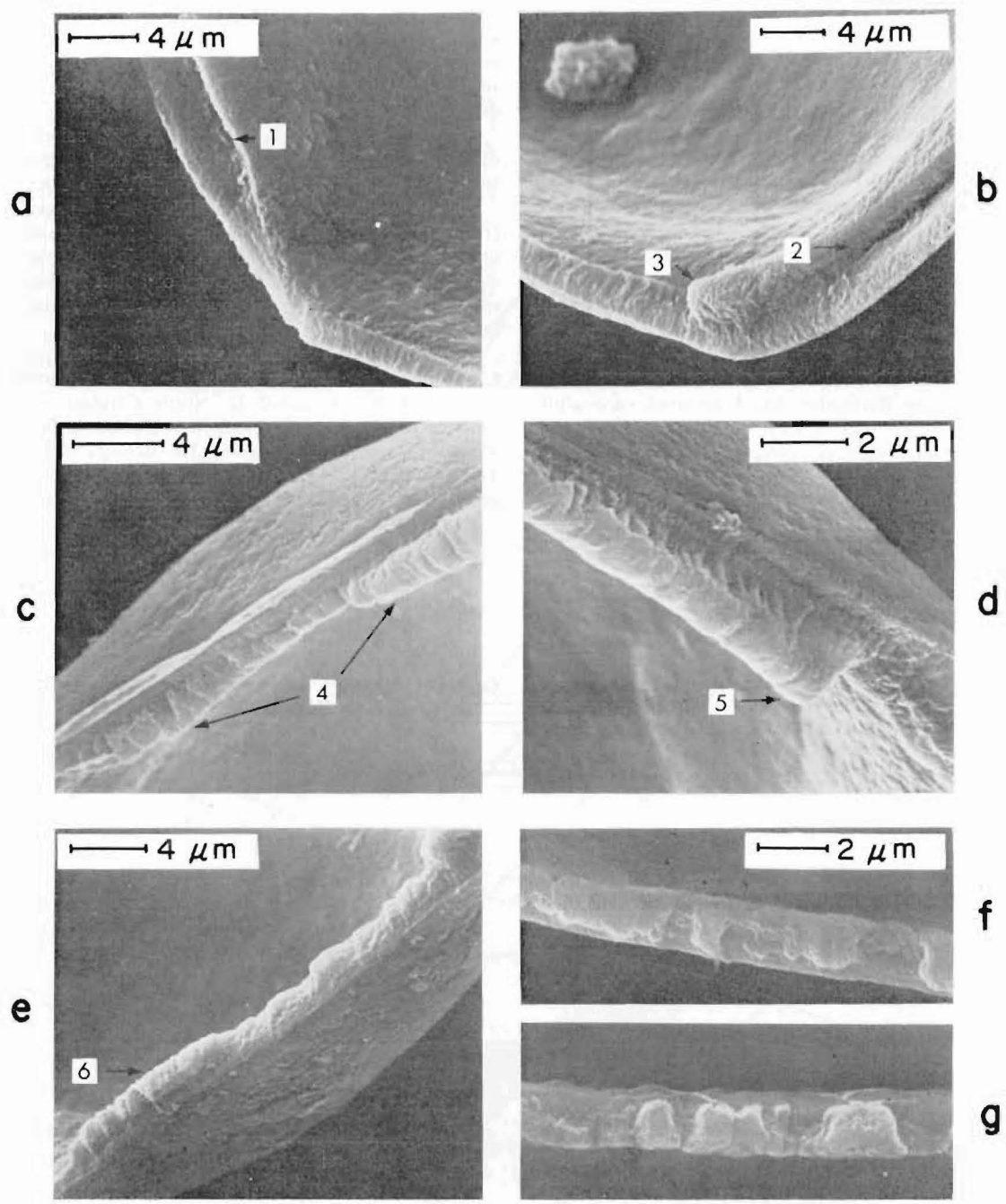

Fig. 5. Scanning electron micrographs of larval hinge of *Chione stutchburyi*. (**a–e**) late stage larvae, L = 180–200 μm: (a), posterior shoulder of right valve, showing lateral hinge groove (1) (×3130); (b), anterior shoulder of right valve, showing lateral hinge groove (2) and lateral tooth (3) (×3130); (c), provinculum of left valve, showing 2 toothed projections (4) (×3770); (d), anterior provincular teeth of left valve (5) (×6340); (e), provinculum of right valve, showing medial series of teeth (6) (×3220). (**f, g**) matching sections of provinculum of young individual (L = 160 μm) (×6530).

(1967) should therefore be applicable to *C. stutchburyi*.

The broadly rounded umbo noted in *C. stutchburyi* is characteristic of the Veneridae (La Barbera & Chanley 1970), as is the general hinge structure, the rough provinculum which gives the impression of numerous incipient teeth, and the long tooth of the anterior left valve provinculum which opposes a solid lateral tooth of the right anterior shoulder on closure (Rees 1950).

One other species of *Chione*, *C. aucklandica* Powell, has been recorded from the New Zealand region (Powell 1976), but it does not occur around the main islands and its distribution appears not to overlap that of *C. stutchburyi* (Powell 1932, 1976).

Powell (1976) lists 14 other venerid genera from New Zealand waters. The success of practical identification of venerid larvae in the plankton depends on description of all other local species. In comparison with these, the general dimensions and especially the hinge length (La Barbera & Chanley 1970) and minor dentition of the provinculum should allow recognition of *Chione stutchburyi* larvae.

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2. DISTRIBUTION OF *C. STUTCHBURYI* IN THE AVON-HEATHCOTE ESTUARY

2.1 INTRODUCTION

Net production is the most important and useful parameter of the energy balance equation (section 1.1.1) to consider first in assessing the role of a species in an ecosystem. It represents the balance of all energy flows in the population, and the energy available for utilisation by the next trophic level. Calculation of production is based on three essential terms: numbers, biomass, and growth - as discussed by Petrusewicz & Macfadyen (1970). These parameters are both spatially and temporally variable and in order to gain a realistic understanding of energy flow through the *C. stutchburyi* population in the Avon-Heathcote Estuary it was necessary to study in detail both distribution and abundance (section 2.2).

The few published accounts of *C. stutchburyi* distribution link it with lower intertidal muddy to sandy flats of protected estuarine areas (Wood, 1962; Larcombe, 1971; Morton & Miller, 1973; Grange, 1977; Richardson *et al.*, 1979), but no detailed attempt to define the factors influencing distribution has been made previously. Section 2.3 of this study is an assessment of the factors influencing distribution of *C. stutchburyi* in the Avon-Heathcote Estuary.

2.2 SURVEY OF SPATIAL DISTRIBUTION

2.2.1 Methods

A survey of the entire Avon-Heathcote Estuary was undertaken during August and September 1977 to assess the macrodistributional pattern of *C. stutchburyi*. Two hundred sites were sampled, along transects of permanent pegs established and maintained by the Christchurch Drainage Board (Fig. 2.1). Transect lines are located 200 m apart, with pegs at intervals of 100 m or less along these lines. Each peg has been accurately surveyed by the Drainage Board so that the exact position of the site and height on the shore of the sample are known.

Quadrats (one of 0.1 m^2 per site) were excavated to a depth greater than that of *C. stutchburyi* (approximately 50 mm) and the sediment washed through a 2.0 mm sieve. Animals were frozen within four hours of collection and maintained at -20°C until analysed.

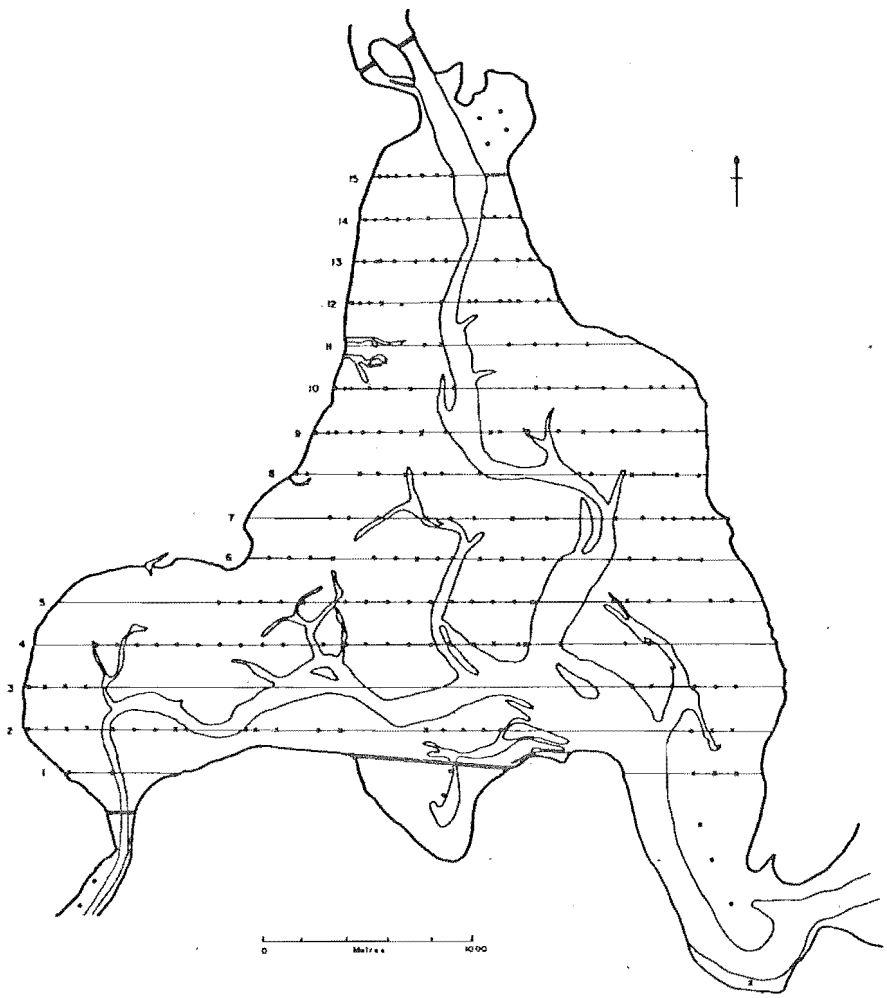


Fig. 2.1 Distribution of survey sample sites in the Avon-Heathcote Estuary.

2.2.2 Density

The number of individuals per quadrat from each site were counted and the density (number m^{-2}) calculated and mapped (Fig. 2.2). The highest density recorded was 3050 m^{-2} in McCormacks Bay, a slightly atypical area in that it has a modified tidal cycle (higher duration of tide cover) and an elevated salinity as a result of the causeway which separates it from the rest of the estuary. The highest density in the estuary proper was just over 2000 m^{-2} (near the Heathcote channel).

In terms of production, the distribution of density is misleading as the size attained by individuals in different parts of the estuary varies considerably. In some cases small individuals are not recently settled young, as might be expected, but can be considered as

sub-populations which appear to reflect poorer growth conditions in their smaller size and some other characteristics such as their thin eroded shells. For example, individuals from near the Heathcote Channel (an area of high density) attain a smaller mean total shell length than do individuals from Moncks Bay of similar age (Fig. 2.3). To compensate for this variation, consideration of size or weight (biomass) is necessary.

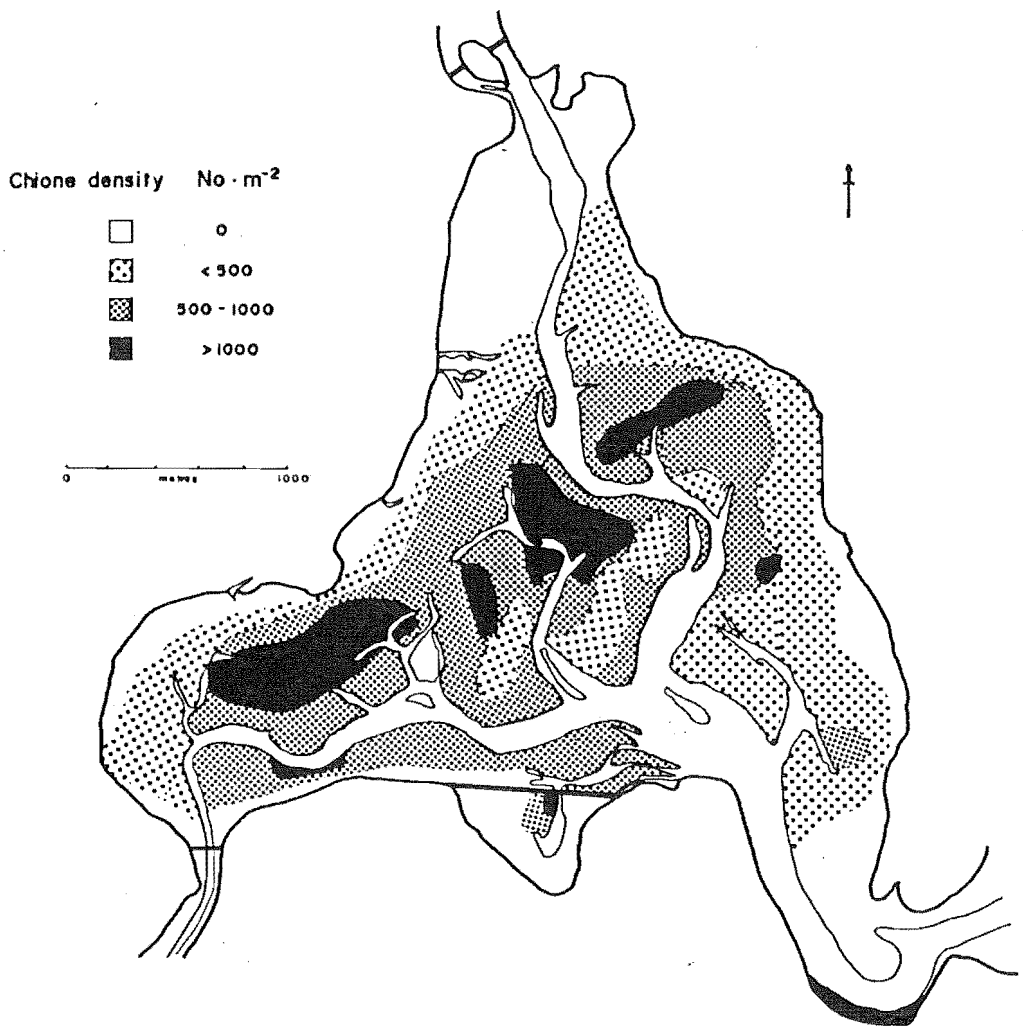


Fig. 2.2 Distribution of density of *C. stutchburyi* in the Avon-Heathcote Estuary.

2.2.3 Biomass

One thousand individuals representing the maximum size range and distribution in the Avon-Heathcote Estuary (from stations indicated by x's, Fig. 2.1) were chosen for investigation of size-weight relationships.

Five shell parameters were measured with Vernier calipers to the nearest 0.1 mm (Fig. 2.4):

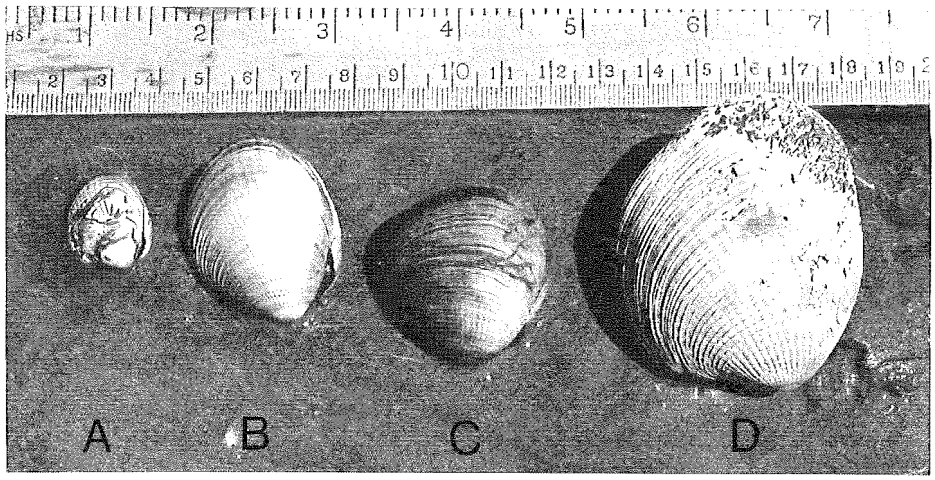


Fig. 2.3 Representative *C. stutchburyi* showing the difference in size attained by different populations. The small individual (A) is typical of those at the mouth of the Heathcote River; the two in the middle are from Redcliffs (B) and Moncks Bay (C); the large shell (D) was found buried and is thought to have existed prior to settlement of the drainage basin.

(1) ligament length,

(2) umbo length (maximum distance from the umbo to the posterior margin of the shell),

(3) total length (maximum anterior/posterior length),

(4) height (maximum dorsal/ventral measurement), and

(5) thickness or breadth (maximum lateral measurement).

The following weights were recorded for flesh and shell of each individual separately:

(1) wet weight after draining for about 20 minutes,

(2) dry weight at 70°C until constant (48 hours), and

(3) ash weight after three hours at 500°C.

A relationship was sought between a shell parameter, and weight which would allow biomass calculations based upon shell measurements alone.

As expected, wet and dry weights were highly variable; wet weight due to variable water content and dry weight because of a variable inorganic ash content (presumably mainly due to sand in the mantle cavity and digestive tract).

Ash-free dry weight, or the organic portion of the animal lost on ignition at 500°C for three hours was considered to be the best weight to use in relating size and weight.

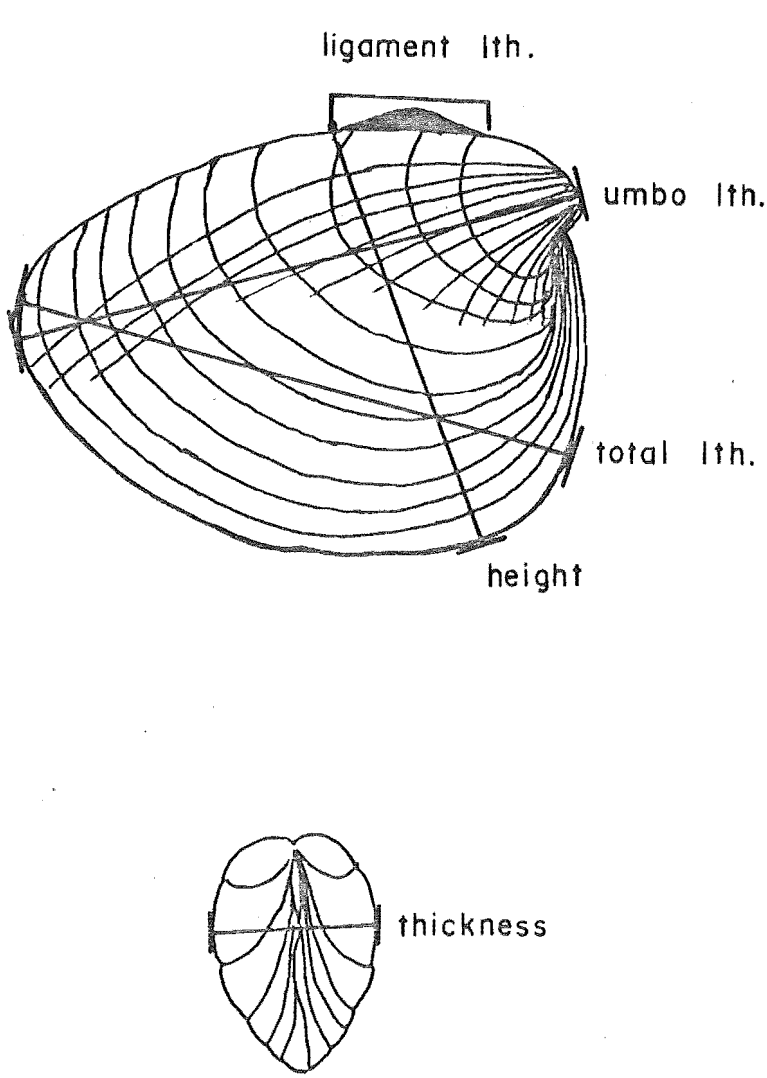


Fig. 2.4 Measurements of *C. stutchburyi* shell parameters.

The ash-free dry shell weight amounts to approximately 5% of the dry shell and 3% of the wet shell weight, whereas ash-free dry flesh weight is approximately 77% of the dry flesh weight and 10% of the wet flesh weight (Table 2.1). These are only approximations as the wet and dry weights were variable.

The proportion of the total biomass attributable to flesh or shell was different, depending upon the size of the individual, and the area from which it was taken. While the ash-free dry weight of the shell accounted for an average of 61% of the total ash-free dry weight (Table 2.1), this was subject to a high (18%) standard deviation on an individual basis for the total sample, but lower (less than 20% in all cases) on an area or sample site basis. This suggests different rates of shell to flesh growth in different parts of the estuary (see section 4.4).

Table 2.1 Relationship between wet, dry and ash-free dry weights for flesh and shell of *C. stutchburyi* of the Avon-Heathcote Estuary.

	Mean	SD	n
$\frac{\text{Ash-free dry shell}}{\text{dry shell}}$	0.08	0.09	994
$\frac{\text{Ash-free dry shell}}{\text{wet shell}}$	0.05	0.06	355
$\frac{\text{Ash-free dry flesh}}{\text{dry flesh}}$	0.77	0.14	989
$\frac{\text{Ash-free dry flesh}}{\text{wet flesh}}$	0.10	0.06	588
$\frac{\text{Ash-free dry shell}}{\text{total ash-free dry wt.}}$	0.61	0.18	998
$\frac{\text{Ash-free dry flesh}}{\text{total ash-free dry wt.}}$	0.38	0.18	998

When regression analysis was carried out on total ash-free dry weight and the five shell parameters, some definite relationships were found. Using the untransformed variables of breadth (shell thickness) and ash-free dry weight, a linear relationship is found to be statistically very highly significant (TAF = .037 Th -0.27, r = 0.82). When plotted, however (Fig. 2.5), the data exhibit a definite curve. Transformation of the shell parameters was attempted and a relationship between the square of shell height and total ash-free dry weight was found to be statistically better than the previous relationship (TAF = 7.9×10^{-4} Ht^2 -.05, r = 0.85). Traditionally, logarithmic relationships have been cited in bivalve size/weight studies (e.g. Ansell, 1964). A plot of untransformed total length against total ash-free dry weight (Fig. 2.6) suggests a logarithmic relationship, and on transformation this relationship is apparent (Fig. 2.7). The linear equation derived from these data;

$$\log_{10} W = 2.78 \log_{10} L - 4.52$$

$$(\ln W = 2.7 \ln L - 10.29)$$

is highly significant (multiple correlation coefficient = 0.87, standard error of the regression coefficient = 1.7%).

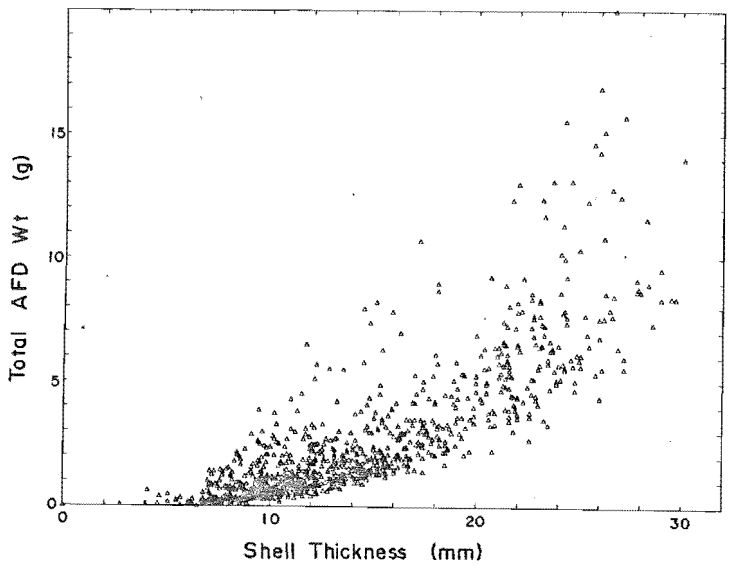


Fig. 2.5 Total ash-free dry weight (g) plotted against shell thickness (mm) for *C. stutchburyi* from the Avon-Heathcote Estuary.

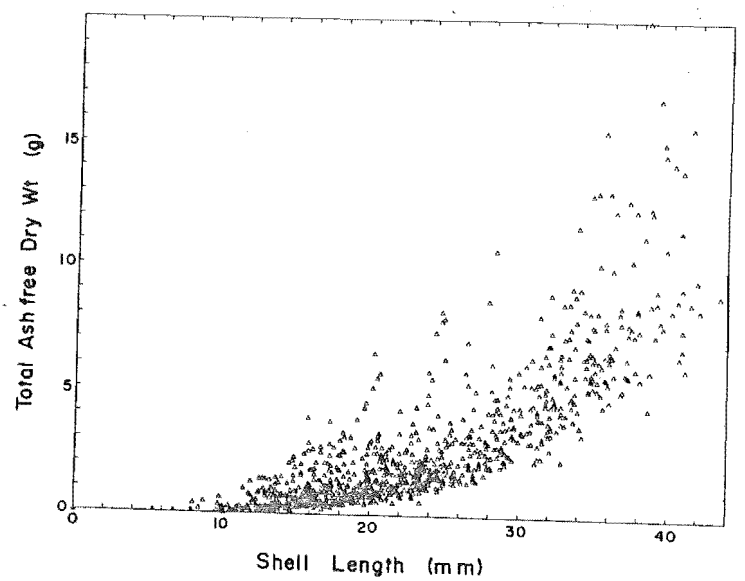


Fig. 2.6 Total ash-free dry weight (g) vs total length (untransformed data); *C. stutchburyi* from the Avon-Heathcote Estuary.

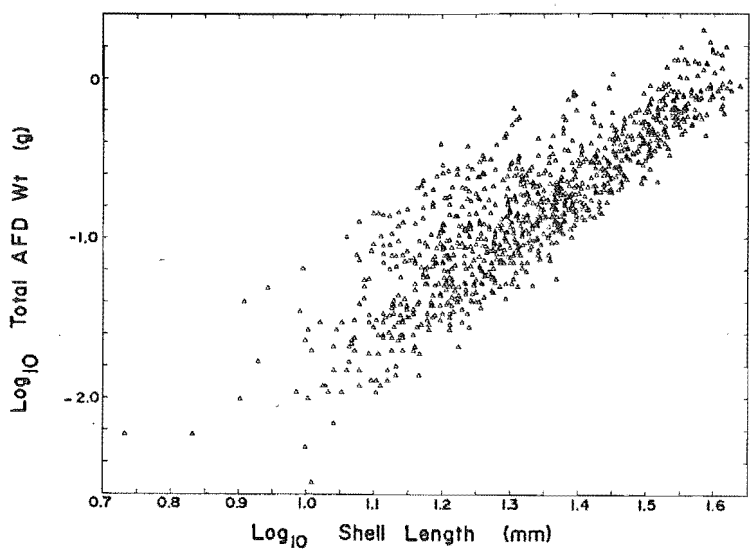


Fig. 2.7 Relationship between $\log_{10}$ shell length and $\log_{10}$ total ash-free dry weight; *C. stutchburyi* from the Avon-Heathcote Estuary.

Because the animals were collected during August and September, the weights discussed in this survey are "winter weights" and are unaffected by gonad development. Larcombe (1971) noted that a period of non-breeding "winter condition" in which there is no growth of the animal, exists for the six winter months.

In light of the wide variety of sizes and apparent growth rates of the animals examined, this length/weight relationship becomes even more useful, in that it should be applicable to animals from other areas. It has the value of allowing a rapid estimate of animal biomass without sacrificing animals, or from shells without animals, as for instance from shell deposits.

By applying this relationship to shell lengths of all other individuals collected in the survey, estimates of the biomass as total ash-free dry weight per m^2 (TAFDWt m^{-2}) were made for each sample site. In Fig. 2.8 the distribution of *C. stutchburyi* biomass has been mapped. The highest biomass recorded was 1200 g m^{-2} (in the two most easterly black areas) although most of the estuary supports a biomass of less than 500 g m^{-2}. Referring to Fig. 2.2, it is apparent that the areas of greatest density and areas of greatest biomass are different. This is illustrated in a plot of biomass against density (Fig. 2.9), showing the range of these two characters and suggesting a difference in growth rates in the estuary.

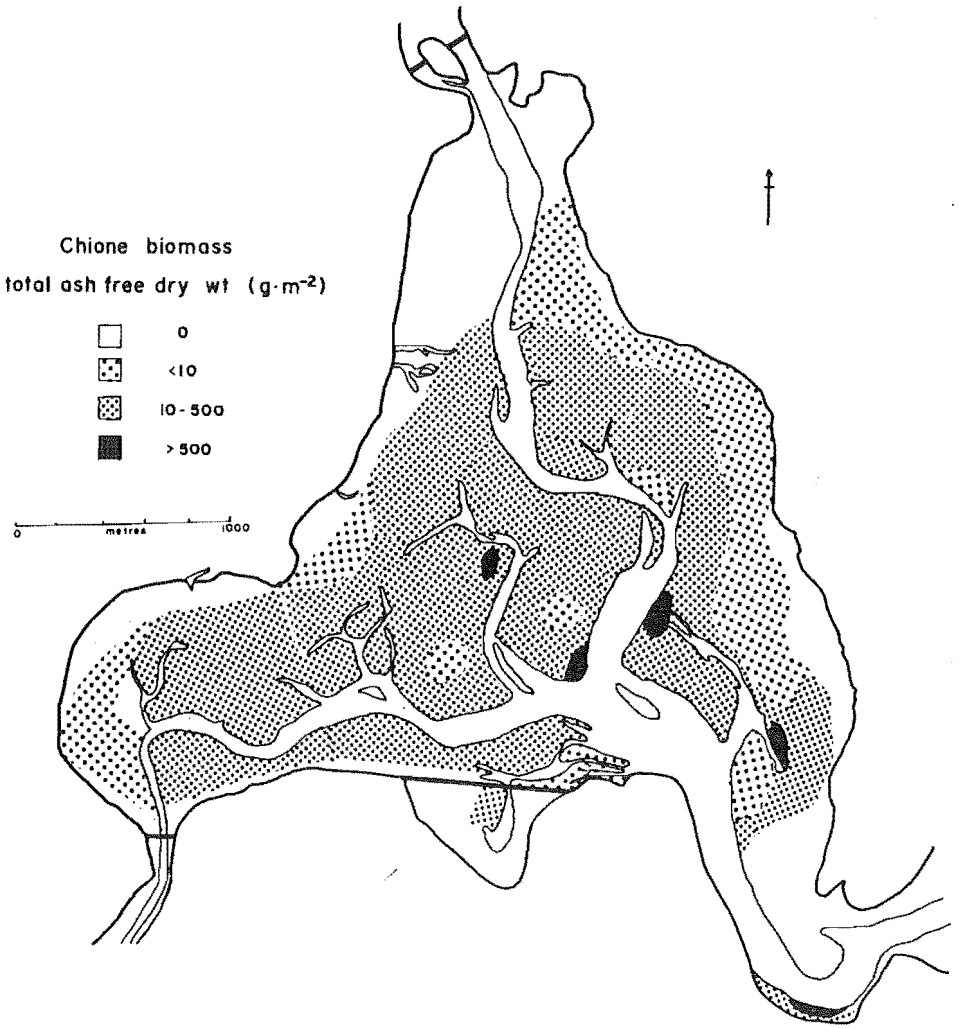


Fig. 2.8 Distribution of *C. stutchburyi* biomass in the Avon-Heathcote Estuary.

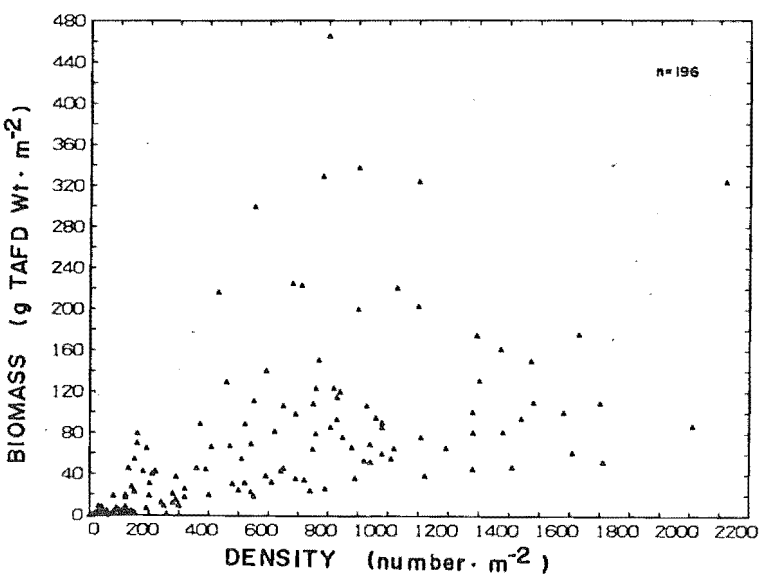


Fig. 2.9 Biomass vs density of *C. stutchburyi* from the Avon-Heathcote Estuary.

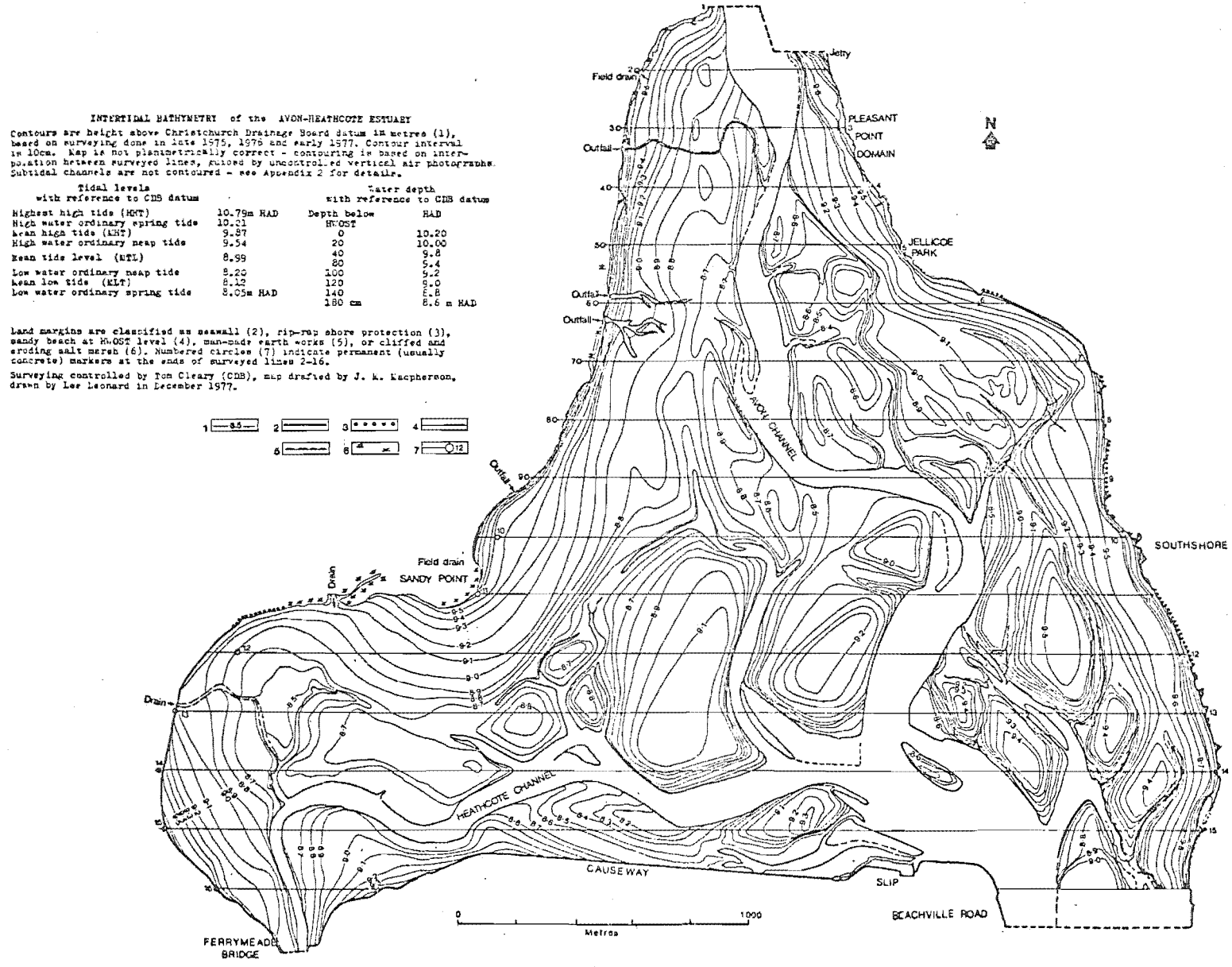


Fig. 2.10 Intertidal bathymetry of the Avon-Heathcote Estuary. From Macpherson, 1978.

2.3 FACTORS INFLUENCING THE DISTRIBUTION OF *C. STUTCHBURYI*

Descriptions of marine benthic animal distribution patterns have accumulated as a result of the emphasis that has been placed on marine littoral surveys for many years; and it is tempting, as data accumulate, to speculate as to the processes responsible for such patterns.

Animal distributions and associations have been based on the correlation of density, biomass and species numbers with a number of biotic factors (Dayton & Hessler, 1972; Campbell & Meadows, 1974; Moore, 1975) and physical parameters, including sediment characteristics (Gray, 1974; Kinner *et al.*, 1974, Rhoads, 1974; Christie, 1975; Grange, 1977) and salinity (Newell, 1964; Wildish, 1970; Boesch, 1972; Wolff, 1974).

Wildish (1977) suggested the use of a hierarchy of multiple limiting physical and biotic factors for study of the controls governing community composition, biomass and productivity. For sublittoral macrofauna, "colonising larval supply and interspecific competition are the major factors controlling composition if temperature and salinity differences are removed. The major factor controlling biomass and productivity is the food supply" (Wildish, 1977).

In the case of a short-siphoned, relatively immobile, shallow burrowing filter feeder, such as *C. stutchburyi*, living in an intertidal area it was hypothesized that period of exposure and sediment parameters would be two of the most important factors affecting distribution.

Woods reported small *C. stutchburyi* at the high shore of a neap flat and larger animals lower on the shore at Howick (cited in Morton & Miller, 1973) and a positive relationship between size and period of immersion has been noted previously for *C. stutchburyi* by Larcombe (1971 - in a number of localities from Otago Harbour to Whangateau Harbour) and by Richardson *et al.* (1979 - in Pauatahanui Inlet). Such a relationship has also been demonstrated for the European cockle, *Cerastoderma edule* (Kristensen, 1957; Hancock & Simpson, 1962) and for other marine groups including polychaetes (Dales, 1952), chitons (Boyle, 1970) and gastropods (Edwards, 1969; Vermeij, 1972; Bertness, 1977).

The importance of sediment type to the distribution of benthic species has often been emphasised. Thorson (1957) summarised the relationship between environmental factors, especially the composition of the bottom substrate, and benthic community composition, and many

workers have reported that suspension feeders are abundant in well sorted fine grain deposits, but that they decrease in abundance as silt-clay content increases (Gray, 1974). Organisms have been noted to modify the environment in which they live to some extent, and this is particularly true of those like cockles living in soft sediments (Rhoads, 1974; Gray, 1974).

C. stutchburyi at Pauatahanui Inlet were found in sediments ranging from a mean grain size of 4.2 Ø (coarse silt) to 1.0 Ø (coarse sand) (Richardson *et al.*, 1979), and Grange (1977) gives an optimum grain size for *C. stutchburyi* at Manukau Harbour of 2.0 Ø.

This study provided an excellent opportunity to investigate the relationship of *C. stutchburyi* distribution to physical characteristics of the Avon-Heathcote Estuary because of data available on exposure (Christchurch Drainage Board, unpubl. data) and sediment parameters (Macpherson, 1978 and unpubl. data) at sites along the same transects sampled in this study.

Surveys of the peg lines undertaken by the Christchurch Drainage Board allowed construction of a map of intertidal bathymetry of the Avon-Heathocte Estuary by Macpherson (1978 - reproduced as Fig. 2.10) with a 10 cm contour interval.

Tide records from a Lee Recorder located at the Heathcote Bridge (Christchurch Drainage Board, unpubl. data) allowed calculation of the tidal cover and exposure at all levels on the shore. The mean curves of four tides surrounding the extreme spring (21 July) and neap (E(L)H neap) (25-26 October) for 1978 are presented in Fig. 2.11). Hours of exposure are plotted against the height above Christchurch Drainage Board datum in metres. These are extremes; all other tides would lie within the curves. Height above Christchurch Drainage Board datum is related to state of tide as follows (Christchurch Drainage Board, unpubl. data; Macpherson, 1978):

tide	height above datum (HAD in metres)
MHW Spring	10.21
MHW Neap	9.54
Mean Tide Level	8.99
MLW Neap	8.20
MLW Spring	8.05

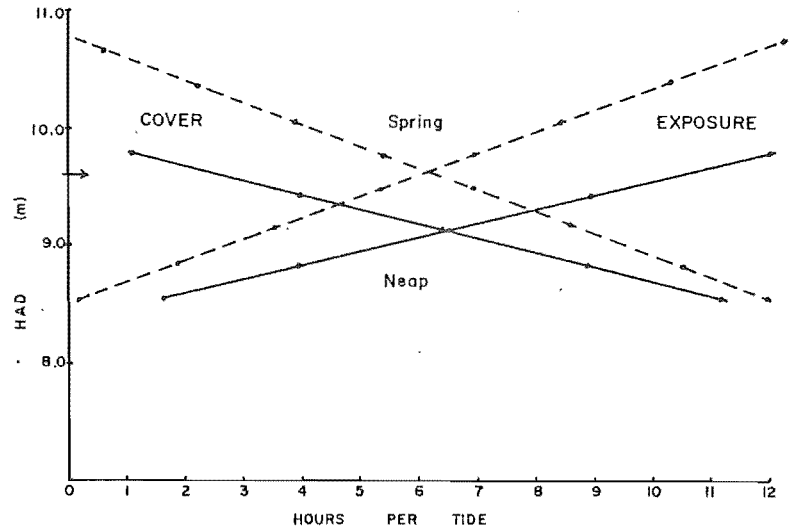


Fig. 2.11 Hours of exposure and cover vs height on the shore for extreme tide of 1978; Avon-Heathcote Estuary.

Sediment parameters, based on particle size were measured by Macpherson (1978 and unpubl. data). The "mud" fraction is the dry weight of sediment which passes through a sieve of 4 Ø (where Ø = the negative $\log_2$ of the grain size in mm; Fig. 2.12) mesh diameter, as a percent of the dry weight of the total sample. The "sand" fraction was analysed in a Woods Hole type rapid sediment analyser (Macpherson, 1978), measuring the settling rate of particles. "Mean" and "median" Ø values and the "degree of sorting" which is a measure of the standard deviation of the sand fraction analysis were also calculated.

Particle size analysis

SHELL	S A N D		
	Medium sand	Fine sand	Very fine sand
<0.5 mm	0.5-0.25 mm	0.25-0.125 mm	0.125-0.063 mm
<1 Ø	2 Ø	3 Ø	4 Ø

M U D						
SILT				CLAY		
63-31 μ	31-16 μ	16-8 μ	8-4 μ	4-2 μ	2-1 μ	<1 μ
5 Ø	6 Ø	7 Ø	8 Ø	9 Ø	10 Ø	10-14 Ø

Fig. 2.12 Particle size groupings used for sediment analysis.

Sediment samples were taken to a depth of not more than 2.0 mm. This is considered preferable to the common practice of sampling the top 50 mm or so for the following reasons:

(1) The Avon-Heathcote Estuary is in a net state of erosion, rather than deposition, and it was felt that the thin "active" surface layer was more likely to reflect contemporary environmental changes than was subsurface sediment (Macpherson, 1978; Macpherson & Lewis, 1978), and

(2) *C. stutchburyi*, with its extremely short siphons, is likely to be affected more by this zone in terms of resuspended, and therefore potentially ingested, particulate matter (section 4.8).

Eighty-nine stations, representing a full range of sediment and tidal characteristics, and for which all of the parameters had been measured, were used in an attempt to relate distribution of *C. stutchburyi* (density and biomass) to tidal position (height above datum) and sediment parameters (% mud, mean and median particle size, and degree of sorting).

Plots were made of each of the above environmental parameters against both biomass and density (for example, Figs. 2.13, 2.14, 2.15). In all cases, a wide scatter in both biomass and density was apparent over much of the range of the factor inhabited by *C. stutchburyi*. For example, Fig. 2.13 shows clearly that there is a great variation in the biomass and density of cockles over most of the tidal range and also that there are a number of stations with no cockles over the entire range of tidal height.

As the scatter was common to plots of all parameters, I hypothesised that it could be the result of several factors acting simultaneously.

The problem of isolating component factors in the distribution of *Chione* led me to a theoretical consideration of the distribution of organisms in the estuarine environment.

It involves assessing factors on two functional levels. The first is a PRESENCE/ABSENCE level which defines only the limit of TOLERANCE to a particular factor on a presence or absence basis. This is the level of assessment common to the limiting factor approach presented for example in Macan (1963) and Krebs (1972).

The second level is the INTENSITY level which is reflected in the pattern of arrangement, or in this case growth or production (density and biomass) of organisms within the zone of occupation.

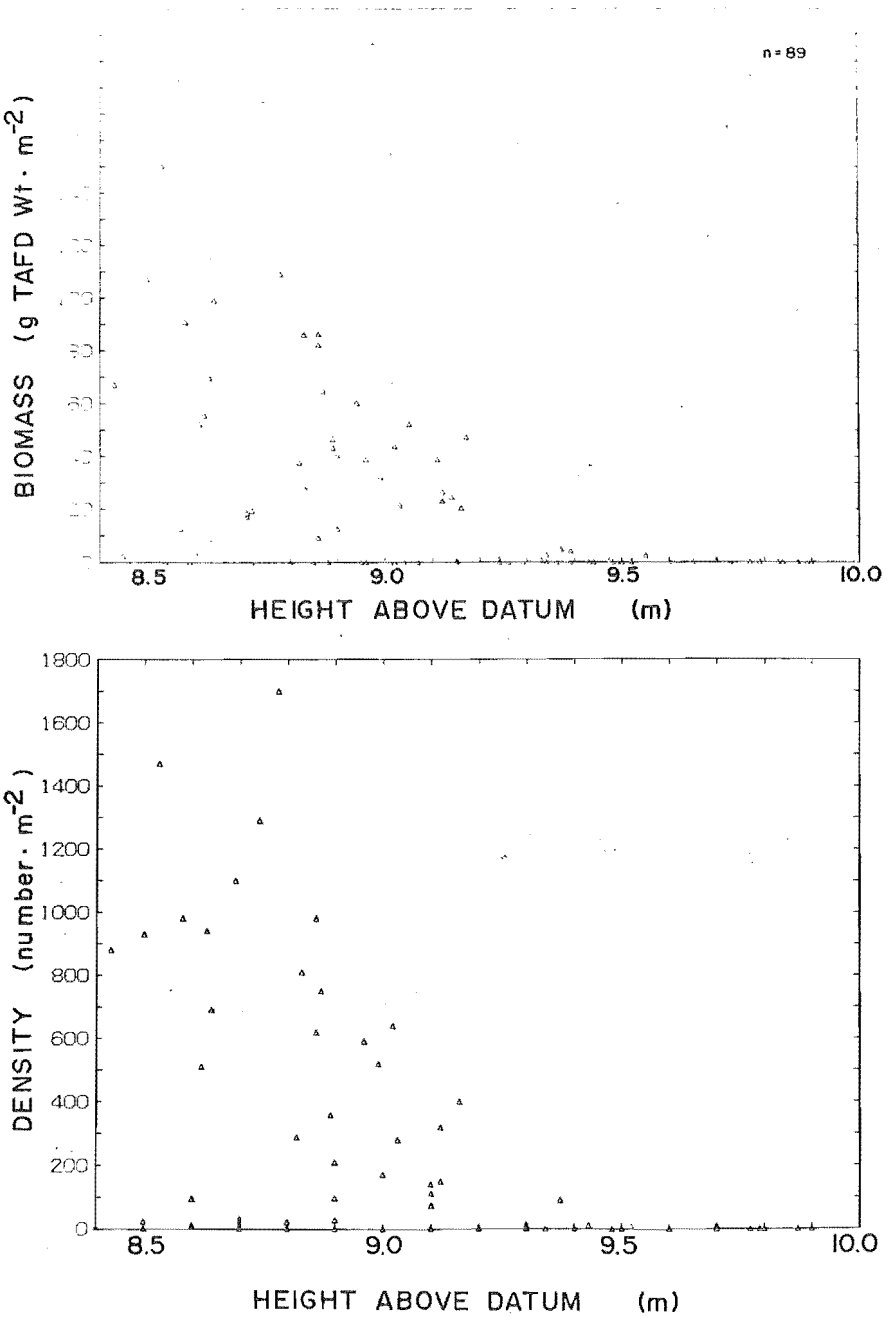


Fig. 2.13 Plot of *C. stutchburyi* density and biomass against height above Christchurch Drainage Board datum (n = 89).

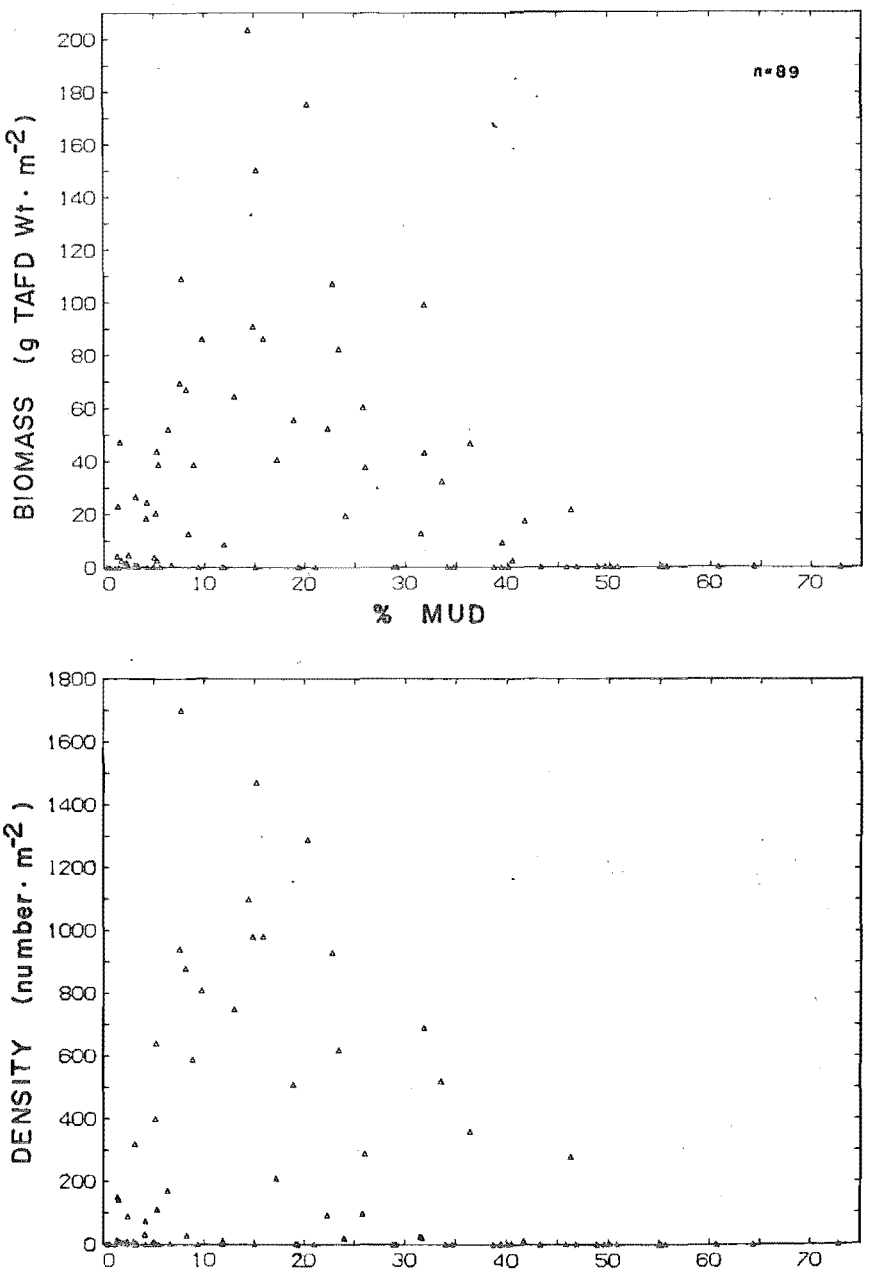


Fig. 2.14 Plot of *C. stutchburyi* density and biomass against mud content of the sediment (n = 89).

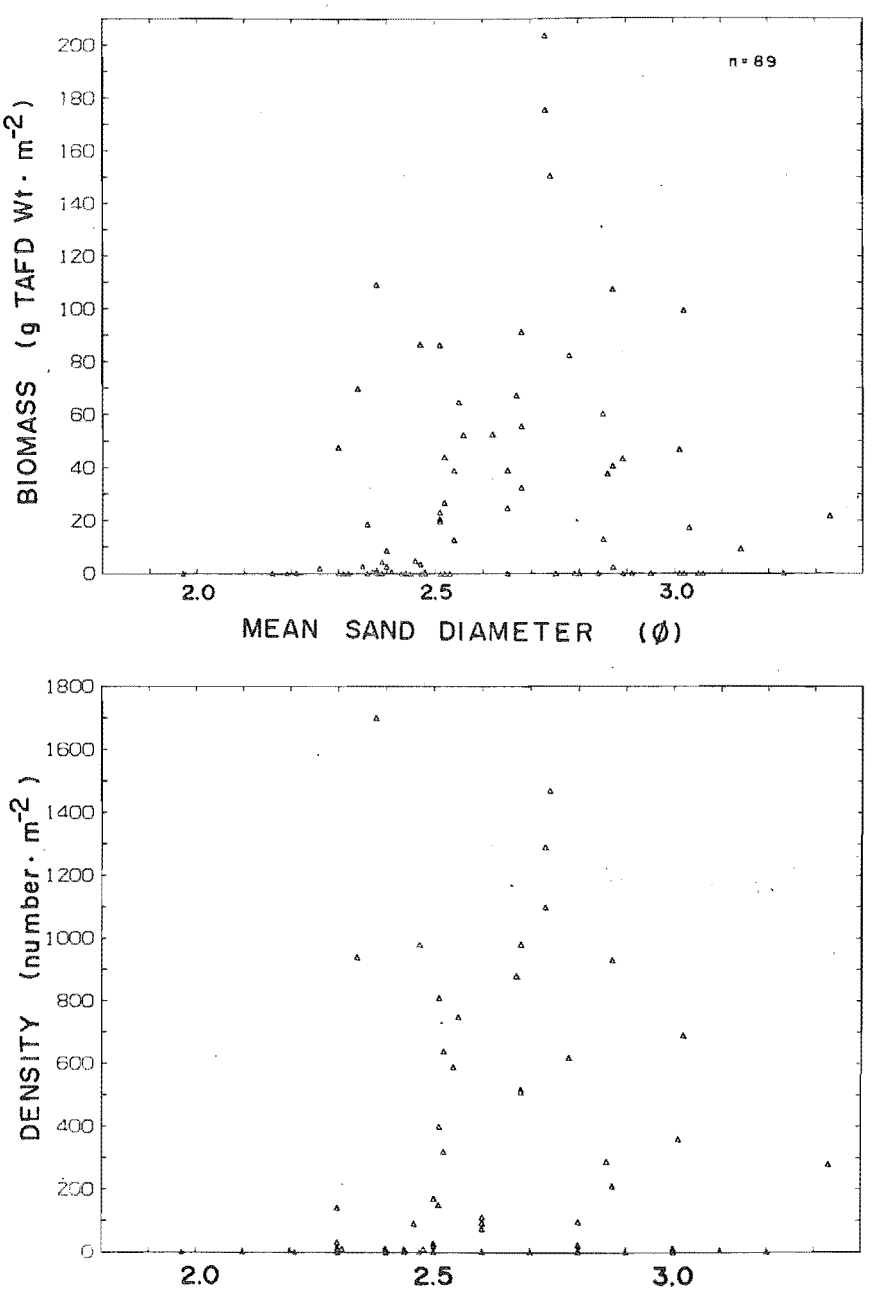


Fig. 2.15 Plot of *C. stutchburyi* density and biomass against mean sand grain diameter of the sediment (n = 89).

Fig. 2.16 is a theoretical one comparing animal presence with an evnironmental gradient. As is indicated in the left line, the zone of tolerance is restricted in response to interspecific competition (in highly competitive situations, such as rocky shores). Opposing this is the non-competitive situation in which as a result of plasticity, the organism expands its distribution within the zone of tolerance and reflects the more drastic conditions in its presence: with fewer numbers, smaller size etc.

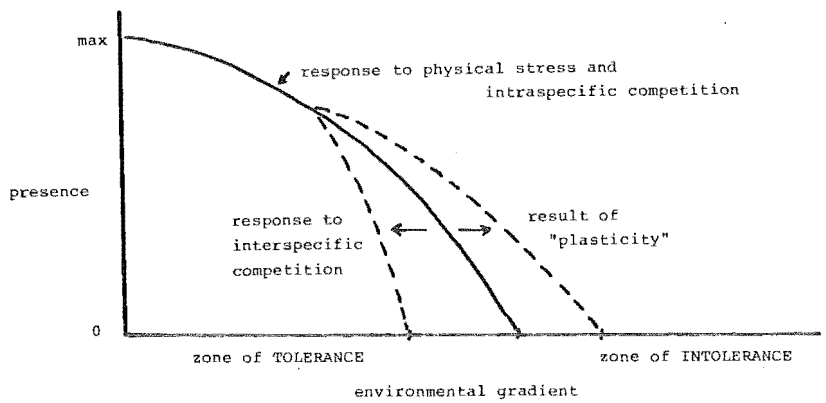


Fig. 2.16 Theoretical curve of animal presence along an environmental gradient.

I have applied this two-level approach to test the relationship between tidal and sediment parameters and *C. stutchburyi* distribution as follows.

Four criteria limiting the absolute distribution were identified from plots of all stations at the presence/absence level. The first (Fig. 2.13) is height above datum - the critical level being 9.6 m. The second (Fig. 2.14) is mud - no individuals were found in areas with greater than 50% mud. This may have to do with the incompatibility of very fine particles and a filter feeding existence. The third (Fig. 2.15) is a mean diameter of the sand fraction greater than 2.25 Ø. These are coarse sediments (mostly near the mouth of the estuary and main channels) often subject to disturbance by water movement, and represent an unstable environment.

The final criterion is proximity to the point of oxidation pond discharge; more specifically the area to the north of the discharge pipes,

toward the Avon River. This area has been observed during dye tracer studies of flow to be an area of ponding during the flood tide (Knox & Kilner, 1973). Some sediments in this area are of different origin to the rest of the estuary, representing the last exposed area of a drastic mud deposition which is thought to have occurred during settlement of the drainage basin between 1850 and 1875 (Macpherson, 1978; section 1.2.2). The sediment is typically hard, undisturbed and exhibits finer particles of mud than is typical of the rest of the estuary. The persistence of this atypical situation is enhanced by the fact that it is an area of low wind and wave energy and therefore deposition - especially of fine particulate sediments (Macpherson, 1978; D. Kreuger, pers. comm.).

The absence of *C. stutchburyi* from fifty-one stations was explained according to these criteria (summarised in Table 2.2) and these data were removed for further analysis of cockle distribution.

Table 2.2 Factors limiting the distribution of *C. stutchburyi* in the Avon-Heathcote Estuary.

Critical Factor	Level
1. Tidal level	Above 9.6 m HAD
2. % mud	Above 47.5%
3. Mean diameter of sand particles	Larger than 2.25 Ø
4. Proximity to oxidation pond outfall	

No further stations could be removed by considering either median diameter of the sand fraction, or degree of sorting. As the Avon-Heathcote is microtidal, its sediments are characterised by storm-surge and wave built features (Macpherson, 1978). Tide currents which are normally responsible for transport of large particles are important only near the mouth and low tide channels. As a result, the sediments of most of the estuary exhibit a relatively narrow range of particle size, making the mean and median diameter of the sand fraction similar and the degree of sorting small.

It is interesting to note that most of the stations removed by the level of mud, would also have been removed because of their proximity to the oxidation ponds and it may be that it is the suspended fine particle level associated with the effluent in this area that is critical.

Removal of stations at the presence/absence level then allows analysis (at the intensity level) of distribution at the remaining 48 stations.

Comparison of density and biomass values at a particular site reveal that density exhibits a much greater variation than biomass in relation to an environmental gradient. This does not affect selection of a presence/absence point, but does change the shape of any gradient or continuum of animal distribution within the zone of tolerance. Because of the variation in growth rate, maximum size and density; biomass is considered to reflect more accurately the response to environmental parameters and will be discussed further.

A plot of biomass against height above datum for the remaining 48 stations (Fig. 2.17) reveals a logarithmic decrease in biomass with increasing height on the shore (decreasing time of water cover per tide). From the tide curves (Fig. 2.11) it appears that the zone of tolerance of *C. stutchburyi* is limited by the water cover at the most drastic neap tide. The uppermost limit of distribution (9.6 m) is only 10 cm below extreme (low) high water neap (E(L)HWN) and corresponds to the point on the shore at which the animals would receive a minimum of 1-2 hours water cover on each tide.

The plot of animal biomass against mud content of the sediment (Fig. 2.18) reveals a peak in biomass at stations with a mud content between 10 and 30%; decreasing at higher content (possibly due to limitation by fine particles) and at lower mud content (possibly as a result of sediment instability).

The relationship between biomass and mean sand diameter (Fig. 2.19) reveals a similar peak between 2.5 Ø and 3.0 Ø, although this is not as convincing a plot. Similarly a peak in biomass is evident at a median sand diameter of 2.7 Ø (Fig. 2.20). Plots of the degree of sorting and biomass do not reveal any obvious relationship (Fig. 2.21), probably because this parameter is based upon mean sand diameter, and its range is narrow.

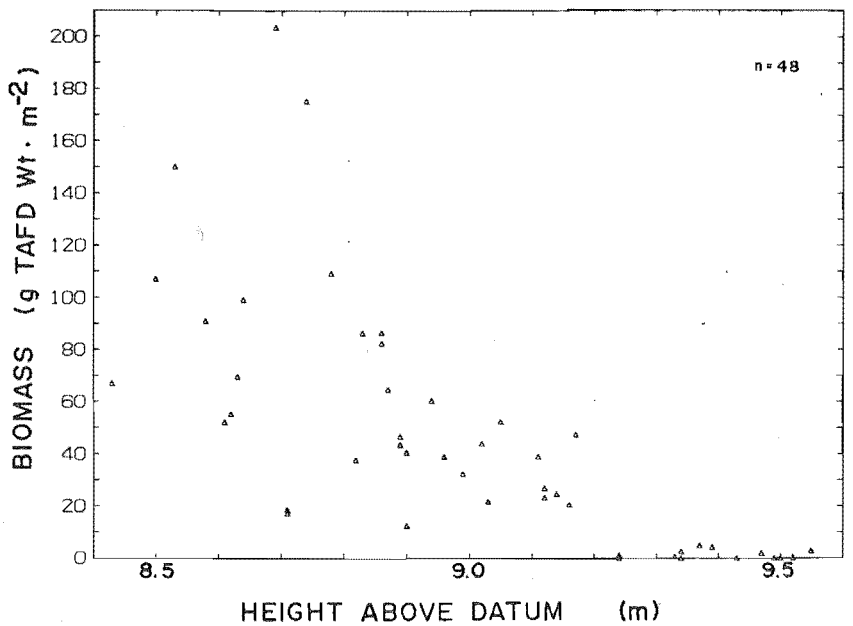


Fig. 2.17 *C. stutchburyi* biomass plotted against position on the shore (n = 48).

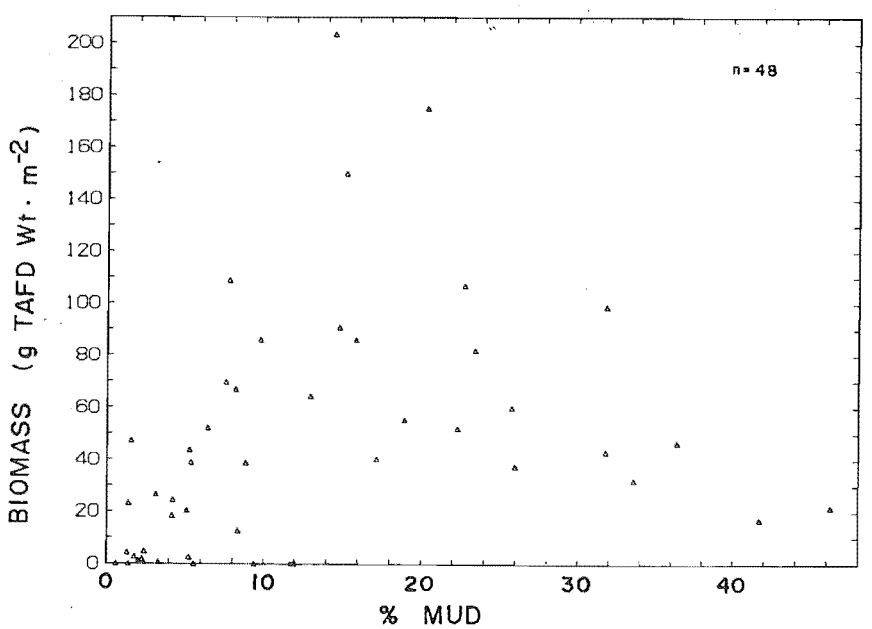


Fig. 2.18 *C. stutchburyi* biomass plotted against mud content of the sediment (n = 48).

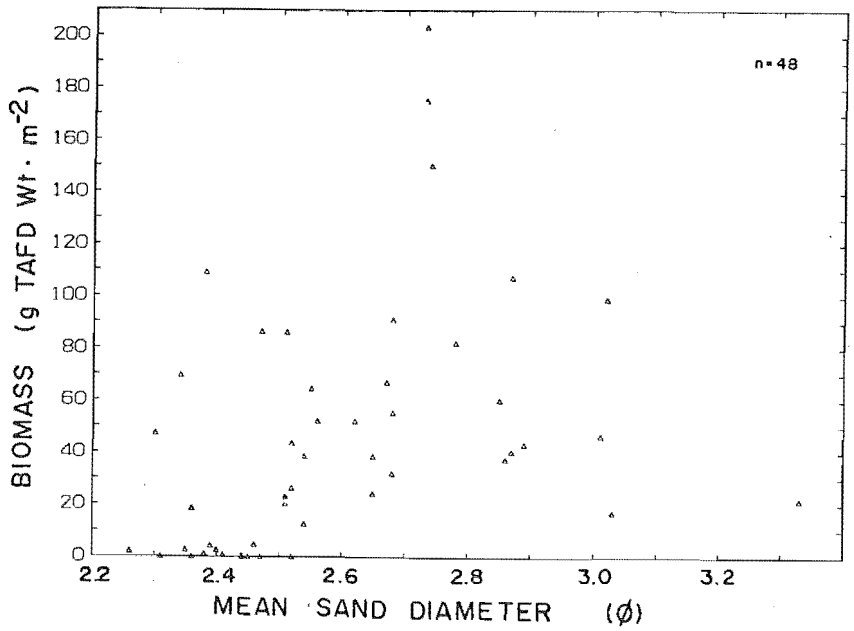


Fig. 2.19 *C. stutchburyi* biomass plotted against mean sand grain size of sediment (n = 48).

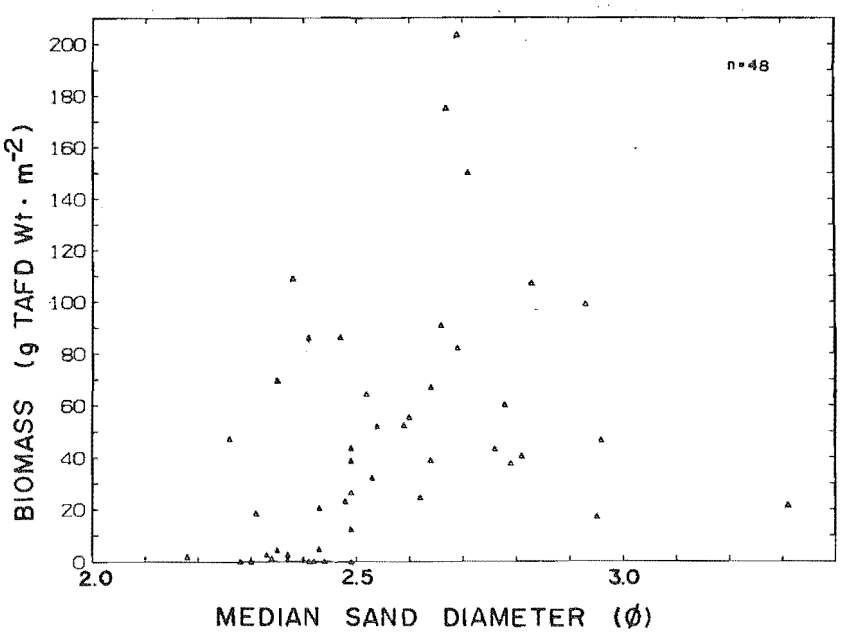


Fig. 2.20 *C. stutchburyi* biomass plotted against median sand grain size (n = 48).

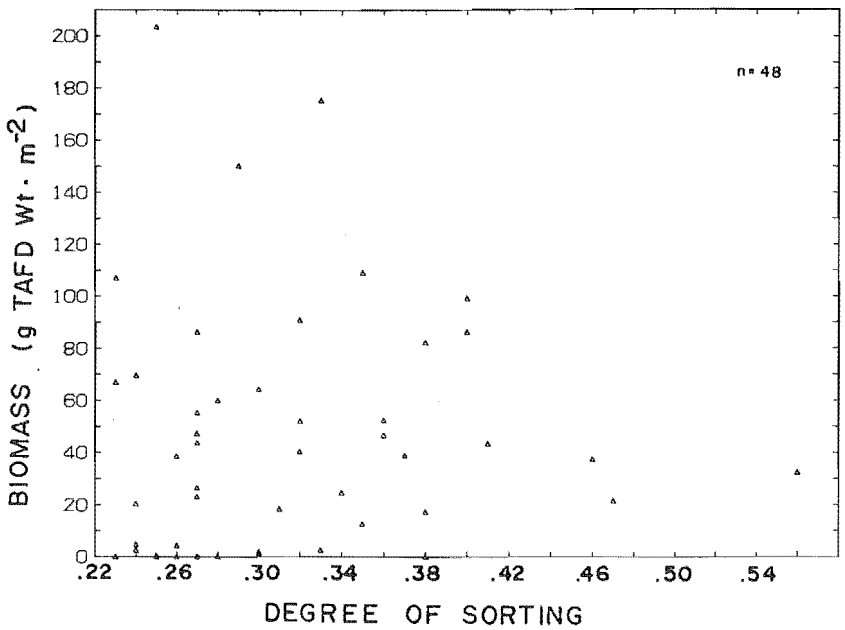


Fig. 2.21 *C. stutchburyi* biomass plotted against the degree of sediment sorting (n = 48).

In summary, the tolerance limits of *C. stutchburyi* (in terms of distribution) were defined for environmental parameters based upon the presence of animals over the range (along a gradient) of each parameter. *C. stutchburyi* was observed to be restricted in its distribution to the shore below the lowest high water neap and to sediments containing less than 50% mud and with a mean sand particle size smaller than 2.25 Ø units in diameter. In addition, *C. stutchburyi* was absent from the area around the point of oxidation pond discharge.

Subsequent consideration of *C. stutchburyi* presence (in terms of biomass) at sites where none of the environmental parameters was limiting allowed investigation of the response of the animal to each factor within the zone of tolerance.

In that number and biomass are not influenced by presence/absence criteria in these plots, or by factors of interspecific competition, I feel that the relationships observed at the intensity level may be thought of as realistic in assessing the "preference" of *Chione* biomass for each particular factor at the levels I have mentioned. Table 2.3 shows the tolerance values and approximate "preference" or the values at which the biomass tends to be greatest for each parameter.

Table 2.3 Tolerance and preference of *C. stutchburyi* to environmental factors in the Avon-Heathcote Estuary.

Factor	Tolerance limit	Preference
HAD (exposure)	9.6 m 10.5 hrs/tide	8.7 m <3 hrs/tide
MUD	50%	10-30%
mean SAND diameter	2.25 Ø	2.5 - 3 Ø
median SAND diameter	--	2.7 Ø
degree of SORTING	--	0.25 - 0.35

Among the general characteristics of estuaries which make them unique are:

(1) estuaries have few species, but high numbers of individuals,

(2) estuaries are high stress environments, with a wide range of abiotic factors, and

(3) estuarine organisms exhibit a great PLASTICITY:
- wide tolerance
- wide variation in growth rate
- wide variation in morphology (size, weight, shape etc.)

Perhaps this "plasticity" is permitted by greatly reduced interspecific competition (as a result of few species), and may be enhanced by greater intraspecific competition as a result of large numbers of the same species. Therefore, in an estuarine environment, a species may be present over the widest possible range of a particular factor, and may in fact be limited by the factor near its margins. For example, there are *stutchburyi* populations in the estuary that live in such a poor set of conditions that they do not reach reproductive maturity even after a number of years.

Consider in contrast to this, the highly competitive situation on a rocky shore, for instance, where species are often restricted to a very narrow range of conditions, where they are most competitive.

It seems logical that the distribution of estuarine organisms should lend itself nicely to a two-step approach. The first being assessment of the factors showing a definite presence/absence point; and the second being analysis of intensity factors within the zone of occupation.

3 POPULATION DYNAMICS OF *C. STUTCHBURYI* IN THE AVON-HEATHCOTE ESTUARY

3.1 POPULATION STRUCTURE

C. stutchburyi shows a marked seasonal variation in growth and the extremely slow shell growth in winter results in the formation of dark rings in the shell (Larcombe, 1971). Coutts (1974) studied shell rings of a *C. stutchburyi* population from Otago Harbour and showed that the dark rings were formed annually during the winter but also that these rings were composed of micro-bands that could not be correlated with either daily or tidal events. Larcombe (1971) compared shells from the length of New Zealand and noted that growth rings are more pronounced in shells of populations from southern areas.

Shell rings were used as the basis of age determination in this study. Shells were cut from the umbo to the lip, and the cut edge ground with carborundum powder on a glass plate. Annual rings were visible as dark blue or purple lines deflecting to the outer margin of the shell. In some shells, winter rings were coincident with a major groove or depression in the outer surface of the shell and were easily counted, especially in the area of the hinge. Some shells were etched with 10% HCl for approximately 20 seconds (or until winter rings were visible) and the rings counted.

One or a combination of these methods were used to age successfully most of the shells examined. However, shells from some areas, especially shells that were very thin or eroded by the polychaete *Polydora* sp. (see section 4.7) were often difficult to age precisely.

An age-length relationship was determined (using Model 2/Bartletts 3-group regression techniques) from the sectioned and etched shells of 149 individuals representing a wide range of sizes and variety of locations (Fig. 3.1):

$$\ln \text{max shell length} = 0.33 \ln \text{age} + 2.75 \quad (n=149, \text{corr. coeff.} = 0.722).$$

Animals as old as 19 years (shell length approximately 40 mm) were recorded. Shells of 10 years of age exhibited the greatest range of length (20 mm at McCormacks Bay to 40 mm at Moncks Bay).

Length-frequency plots of *C. stutchburyi* populations are typically unimodal (Larcombe, 1971; this study), and Larcombe concluded that year

groups could not be identified by peaks on length-frequency curves. The peak about mean adult length usually consists of several year groups. This appears to be due to several factors. Firstly, *C. stutchburyi* populations are often composed of only a narrow range of year classes. Secondly, *C. stutchburyi* has a protracted spawning period resulting in a protracted recruitment and, possibly, size variation among members of the same year class. Thirdly, growth rates are variable. Thus there may be considerable overlap in the lengths of the different age classes.

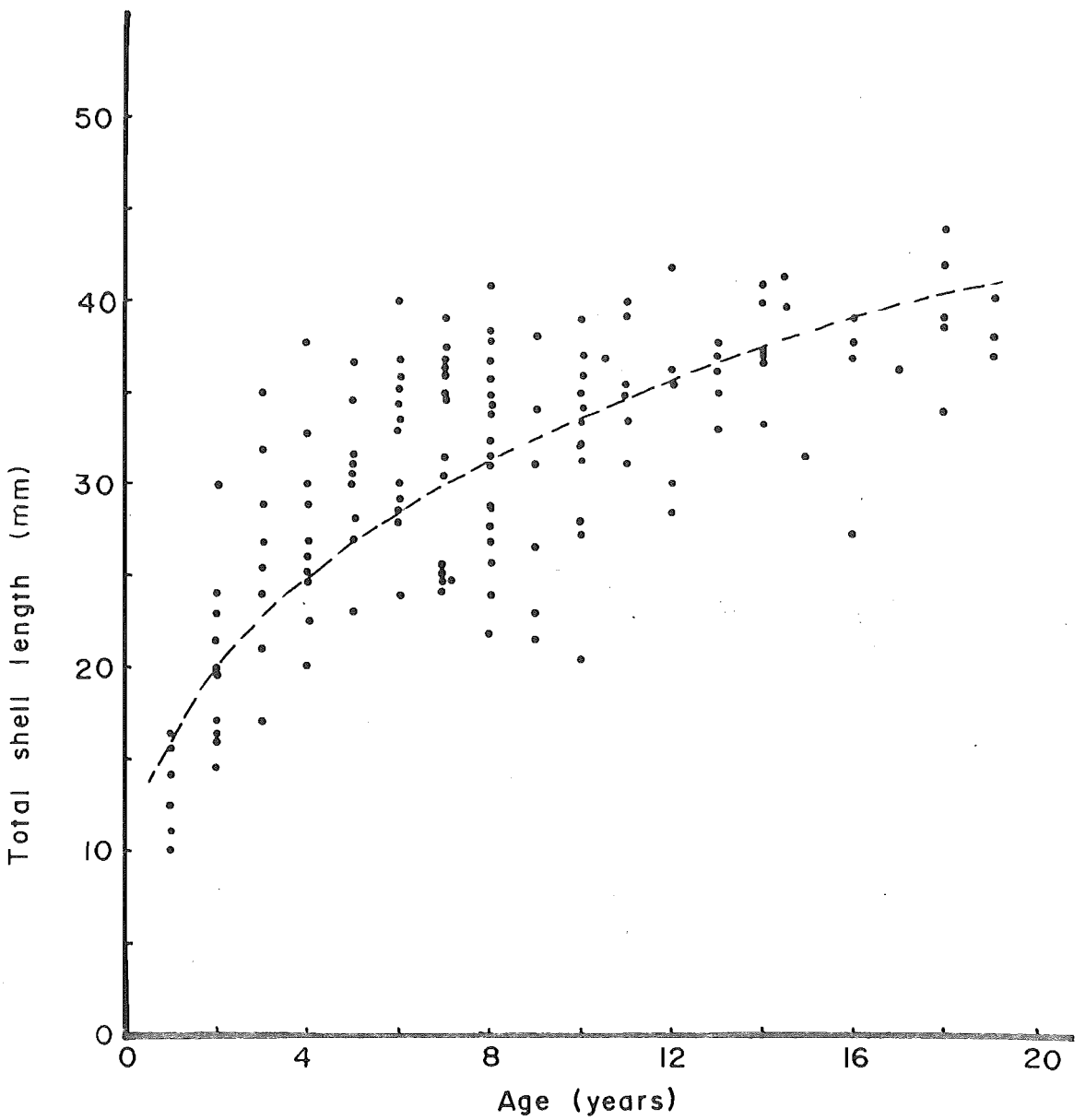


Fig. 3.1 Relationship between age and shell length of *C. stutchburyi* from the Avon-Heathcote Estuary.

The spatial variation in length at a particular age was demonstrated in section 2 (Fig. 2.3). In addition, Larcombe (1971) noted the mean adult length of high shore populations in Whangateau Harbour to be 12 mm, compared with 45 mm for low tide populations of similar age structure.

Spatial variability of growth rate is probably due to environmental influences, and it appears that this is reflected in the mean adult size attained by animals in a particular area. Because of the tendency to a unimodal size and age class distribution, mean shell length is considered to be representative of the population. It is therefore considered to be a useful parameter in comparing the spatial variation of growth of *C. stutchburyi* in the Avon-Heathcote Estuary and is used in calculation of production (section 4.3).

3.2 DENSITY MANIPULATION EXPERIMENTS

3.2.1 Introduction

C. stutchburyi is a relatively long lived species; some individuals surviving for at least 19 years in the Avon-Heathcote Estuary (section 3.1) and more than 20 years in Otago Harbour (Stephenson, unpublished data). The widespread dominance by a single age class or a very few age classes, raises questions about the stability of the population structure, the continuity of recruitment and the reliability of larval settlement.

The adult population structure indicates spatial and temporal variability of net recruitment (those recruits that live to adult size). However, this pattern could be due to a number of factors including planktonic larval survival and distribution, factors influencing settlement of larvae, survival of newly settled spat, dynamics of the "resident" adult population and mortality.

In order to gain some insight into recruitment, larval settlement and survival, and to answer questions about the dynamics of adult populations, density manipulation experiments were carried out in the Avon-Heathcote Estuary. These were designed to investigate:

(1) the association between the presence and density of an established adult population and the settlement and survival of larvae;
(2) the distribution of recruitment in the first year; and
(3) the magnitude of recruitment and mortality in the first year.

In addition, by manipulating the density of adult populations in these experiments, information was obtained on the population dynamics of adult *C. stutchburyi* populations especially with respect to distribution and changes in density.

3.2.2 Methods

Manipulation experiments were set up between September and November 1978, and monitored during the following two spatfall seasons.

Thirteen 9 m^2 quadrats, separated by buffer zones of 3 m, were marked with corner pegs on a gently sloping area of sand/mud flat off South Brighton Spit (Tern Street) (Fig. 3.2). In an attempt to eliminate migration, "Hardiplank" fences were set into the mud to a depth of 20 cm, so that 5 cm was protruding above the sediment surface, around four quadrats (numbers 10 to 13).

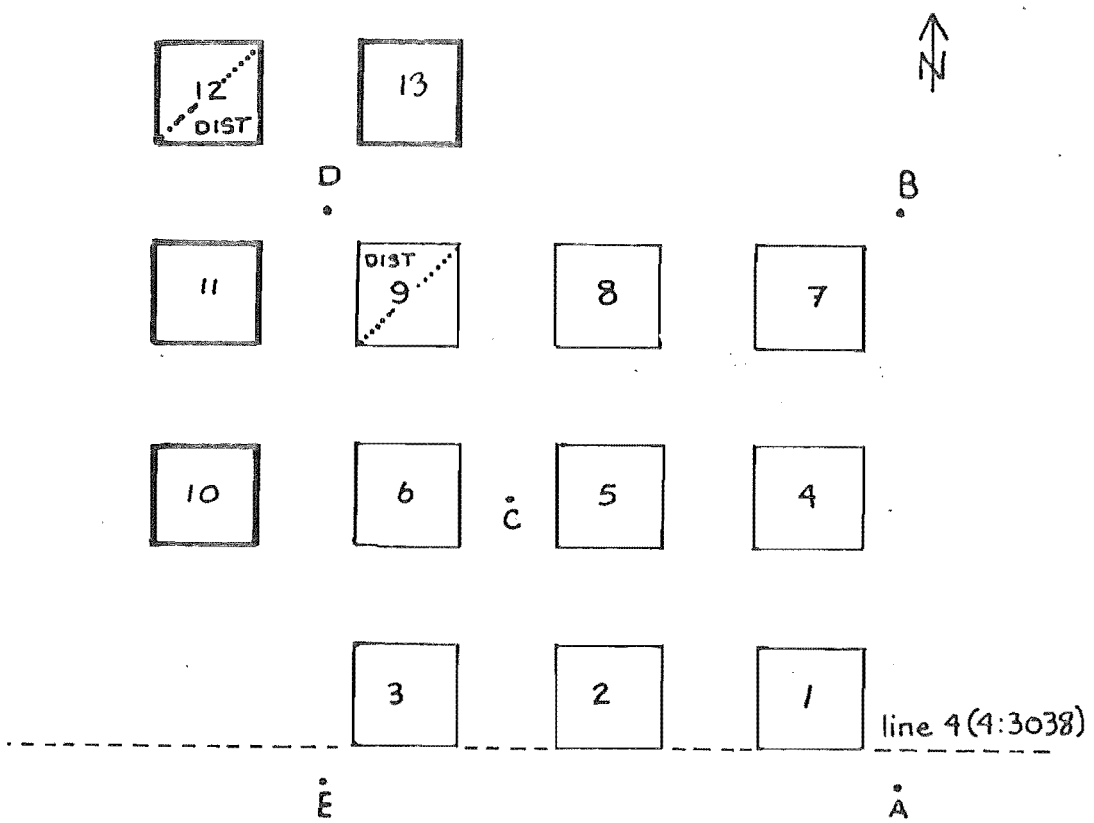


Fig. 3.2 Orientation of density manipulation plots (1 - 13; of 9 m^2 area each) in the Avon-Heathcote Estuary. Treatments are summarised in Table 3.1.

Treatments included (1) complete removal of animals, (2) double density, and (3) normal (control) density; plus controls for disturbance (digging) and fences. Clearing of the quadrats was achieved by removing all sediment (and cockles) to a depth of 50 mm onto a plastic sheet beside the quadrat, followed by sieving sediment through a 2 mm mesh back into the quadrat. A summary of the final treatments is presented in Table 3.1. The quadrats were monitored both for short term effects of disturbance and density on the adult populations, and for long term effects on the resident population and on spatfall and recruitment.

Table 3.1 Summary of density manipulation plot treatments.

Quadrat	Date	Treatment	State
1		untouched	control
2	3/ 9/78	dug only	disturbance control
3	3/ 9/78	dug animals removed	disturbed 0 density
4	3/ 9/78	dug animals from 7 added	disturbed double density
5		untouched	control
6	3/ 9/78	undug animals from 3 added	undisturbed double density
7	3/ 9/78	dug animals removed	disturbed 0 density
8		untouched	control
9	14/11/78	northwest half dug animals from 10 added	part disturbed double density
10	14/11/78	fenced dug animals removed	fenced disturbed 0 density
11	20/11/78	fenced	fence control
12	20/11/78 1/12/78	fenced southeast half dug animals from 13 added	fenced part disturbed double density
13	20/11/78 1/12/78	fenced dug animals removed	fenced disturbed 0 density

3.2.3 Effects of Density Manipulation on Resident Adult Populations

General characteristics of the area

The study area sloped gently from north-east to south-west (the tide line therefore ran through Q 1,5,9,12 etc.). The pattern of density and biomass of the resident populations of the study area was assessed on five 0.1 m quadrats (points A to E, Fig. 3.2). Density ranged from 590 to 1170 m^{-2} (mean = 1008), and estimated biomass from 337.8 to 570.4 gAFDWt m^{-2} (mean = 470.9) (Table 3.2).

Table 3.2 Density and biomass of *C. stutchburyi* in the area of the density manipulation plots (before treatment). Location of samples is shown in Fig. 3.2 (A - E). Biomass is estimated from shell length (Fig. 2.7; section 2.2.3).

Sample	Density number m^{-2}	Estimated biomass g TAFDWt m^{-2}
A	1170	570.4
B	1420	545.7
C	890	411.8
D	970	488.6
E	590	337.8
Mean	900	424.4

Sediment disturbance was accentuated with time. The slight depression left by the removal of animals from Q7 and Q3 was maintained and the bank of cockles on the surface of Q4 resulted in some sediment deposition and the formation of a slight hill.

Disturbance, re-establishment and mortality

Disturbance and reduced density in Q3 and Q7 allowed recolonisation of the quadrats by individuals disturbed along the quadrat margins. After two days, 15 and 20 trails up to 60 cm long were noted in both quadrats. This indicates a maximum observed movement by *C. stutchburyi* of 0.6 m per tide under ideal conditions (i.e. no interference by established individuals). However, these trails were not in a straight

line and very little net movement (< .2 m) occurred. After six weeks, both Q3 and Q7 had some newly established immigrant individuals (especially at the edge) but after 18 months the resident population in these quadrats was still significantly lower than before manipulation (Table 3.3).

Table 3.3 Density of *C. stutchburyi* in the experimental area before and after treatment.

Plot	Estimated original density *	Treatment	Density after treatment †		
			3 months	6 months	9 months
7	30	0 density dug	6	4	3
3	19	0 density dug	1	4	2
5	27	control	27	36	19
2	14	control	11	18	18
4	28	double density dug	46	32	29
6	16	double density dug	24	26	22

* estimated from density outside of plot

† mean of two .025 m^2 samples

Approximately 80 individuals migrated into Q10 (cleared, fenced) in six days, most of these around the edge, especially near one corner of the fence, that had settled to below the sediment surface. It was noted that the mean size of immigrant individuals was smaller than that of the original population or of the resident population around the quadrat, indicating greater mobility of smaller cockles.

Digging did not cause any noticeable mortality in Q2, and re-establishment was complete within six weeks. Similarly, almost all introduced individuals (> 80%) in Q6 (double density, undisturbed) had established themselves within two days and the area was not visibly different from the rest of the mudflat. However, many animals had not

burrowed in Q4 (double density, disturbed) after two days, and even after six weeks many were loose on the sediment surface and some were only half buried. Some loose individuals had rolled up to one metre outside the quadrat. A dense population had been re-established in Q4 which indicated that sediment disturbance did not inhibit re-establishment, but that Q4 probably had too dense a resident population (near maximum?) to allow establishment of all additional individuals after the density was doubled. The density in Q4 after 18 months was approximately 1200 m^{-2} which may represent the maximum sustainable population of animals of this size in this area.

Samples taken after six months and 18 months (Table 3.3) indicated that recolonisation of the 0-density areas (Q7, Q3) was slow. The density after 18 months in each case was less than 15% of the original. Numbers in the double density plots decreased between three and 18 months. The final established density (after 18 months) was near the original in Q4 but higher than the original in Q6.

This experiment indicated that movement of individuals in established populations is minimal. There was only slow re-establishment of cleared quadrats (to less than the original density even after 18 months). Trails in the sediment showed a maximum movement of 0.6 m per tide (even when not hampered by other individuals), and little net movement. Disturbance, in the form of digging, did not result in increased mortality and individuals were able to re-establish themselves, once disturbed.

The only significant increase in mortality following the manipulation experiments was in Q4. There was no indication of increased predation (such as whelks or holes in the shells from oystercatchers). These results from Q4 (double density) indicated that a dense resident population (probably near the maximum sustainable for that area) restricted establishment of further loose individuals. The lack of predation of large individuals which remained exposed on the sediment surface for several months indicates that *C. stutchburyi* may attain a size refuge (see section 4.7).

3.2.4 Settlement and Recruitment

In December 1978 a survey was made of the young-of-year individuals (1978 recruits); defined as those less than or equal to 6 mm total length. The distribution of both the young-of-year and the adult population are shown in Fig. 3.3.

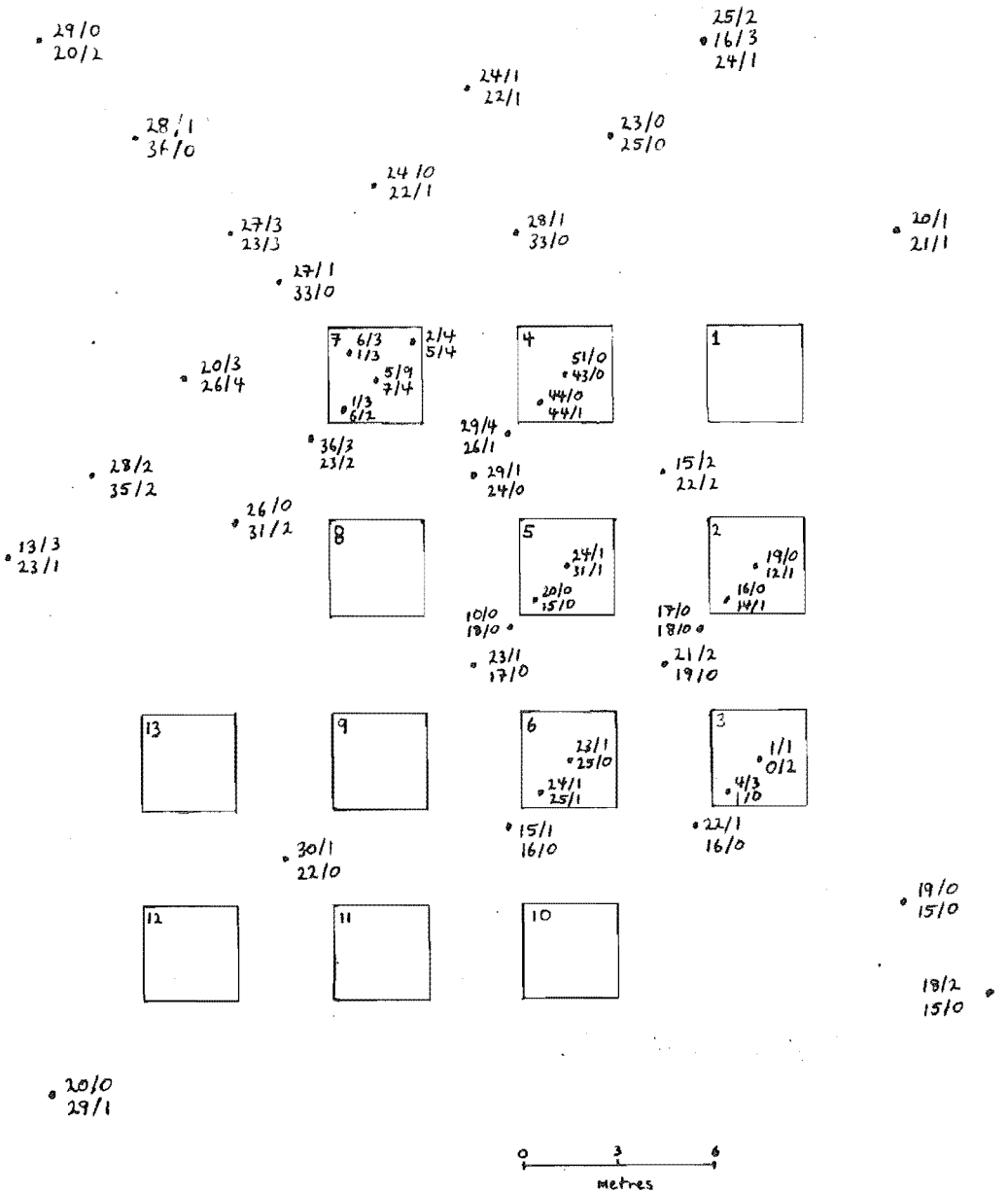


Fig. 3.3 Spatial distribution of adult and juvenile (adult/juvenile numbers per 0.025 m^2 sample) *C. stutchburyi* in the area of the experimental plots; December and January 1978.

The most noticeable feature of this distribution pattern is the high density of young-of-year individuals in and around Q7. The highest number recorded was nine per 0.025 m^2 (360 m^{-2}). Although it would appear as if this high density of juveniles corresponds to low adult density in Q7, this may not be so, for nearby stations of normal adult density (especially to the north) also had high juvenile densities and the other area of 0-density (Q3) did not have noticeably higher young-of-

year density. Further, the area had been cleared for only three months, and any effect on the young-of-year would have to have been on survival of individuals already settled rather than on larval settlement.

Mean density of young-of-year individuals surviving to December 1978 was calculated to be 1.3 per 0.025 m^2 (52 m^{-2}).

In addition to the living individuals, a number of empty juvenile valves were found, and invariably one valve of the pair had a small hole bored in it. This is believed to be a sign of predation by the polychaete *Aonides trifides* (see section 4.7).

Surveys for newly settled *C. stutchburyi* were undertaken at the end of the 1979 and 1980 settlement periods (April). Two, 0.025 m^2 samples were taken approximately 1.5 m inside and 1.5 m outside each quadrat (from the north-west corner in each case) and sieved through a 0.5 mm mesh. The results are tabulated in Table 3.4. Juveniles at this time ranged in size from 0.5 mm to 4 mm, indicating a protracted settlement period. Most were approximately 2 mm.

A corresponding set of sediment samples was taken in 1980 for detailed examination under a dissecting microscope. The surface 10 mm was scraped from a core (3.85×10^{-3} m^2 area) in each quadrat and juveniles less than 2 mm were counted under magnification (Table 3.5).

Estimates obtained in both ways showed spatial variability in settlement (as indicated by those surviving to the end of the settlement period in April). Temporal variability in settlement was inferred from the size range distribution. Settlement numbers (calculated from the mean of two quadrats each of 0.025 m^2 from each site; Table 3.4) ranged from 0 to 160 m^{-2} (mean = 48) in 1979 and from 20 to 680 m^{-2} (mean = 100) in 1980.

Empty valves recorded in 1980 indicated a mortality of about 64 m^{-2} by the end of the spawning season; and suggest a settlement of at least 160 m^{-2} in that year. Samples taken in December 1978 revealed survival of less than 40 m^{-2} young-of-year individuals to that date in most areas; but a very much greater survival (up to 360 m^{-2}) in and around Q7 (Fig. 3.3).

While the two highest settlement records occurred in areas of 0 adult density (Q7, 1978; Q13, 1980) there was no observable increase in settlement in Q1 or Q10. Further, settlement was high around Q7 in 1978 in areas of normal resident adult density. There is very little evidence from these few results for or against the hypothesis that adult density strongly influences settlement.

Table 3.4 Adult and juvenile *C. stutchburyi* density inside (I) and outside (O) the experimental plots; April 1979 and 1980 (mean number in two samples of 0.025 m^2).

Plot	April 1979		April 1980		
	adult	juvenile	adult	juvenile	empty juv. valves
1 I	21	0	18	1.5	2
O	30	2	19	3	1.5
2 I	18	0	19	0.5	2
O	15	1	15	1.5	0.5
3 I	4	0	2	1	3
O	19	0	19	0.5	1.5
4 I	32	4	29	0.5	3
O	28	1	15	2.5	0.5
5 I	33	2	19	3.5	0
O	21	1	19	0.5	2
6 I	26	0	22	0	2
O	17	1	14	4.5	2.5
7 I	4	1	3	2	0
O	24	2	25	2	3
8 I	26	3	24	2	2
O	26	0	24	4.5	3
9 I	23	0	21	3	2
O	24	3	20	0.5	1.5
10 I	0	3	3	3	0.5
O	24	0	24	1.5	2
11 I	28	1	25	1.5	1.5
O	19	2	24	2.5	1.5
12 I	32	1	30	2	1
O	24	0	23	2	0.5
13 I	1	2	4	17	1
O	25	2	21	2	2
mean per quadrat		1.2		2.5	1.6

Variation in recruitment to bivalve populations has been well documented, especially in populations that are the basis of fisheries. For example, Hancock & Simpson (1962) noted abundant settlement of cockles *(Cardium edule)* on Llahrhidian Sands in 1951 and 1958 with only slight recruitment in between.

Table 3.5 Juvenile *C. stutchburyi* density (number per core of area = 3.85×10^{-3} m^2) from the experimental plots; April 1980.

Plot	Total number	Number per size class (mm)		
		1.5 - 2.0	1.0 - 1.5	< 1.0
1	3		1	2
2	1			1
3	0			
4	1			1
5	8		4	4
6	1			1
7	10		1	9
8	2		2	
9	4		1	3
10	2		1	1
11	4		1	3
12	7		6	1
13	10	2	4	4

Larcombe (1971) noted two patterns of recruitment of *C. stutchburyi* in Whangateau Harbour. Recruitment to adult beds was always low but steady, whereas in areas of low adult density high settlement (a few hundred per m^2) was evident.

3.3 MICRODISTRIBUTION

The original survey of *C. stutchburyi* distribution was undertaken on a grid at intervals of 100 - 200 m on transect lines 200 m apart. However, recruitment data (section 3.2.4) and the distribution of resident populations in the experimental plots (section 3.2.3) indicate that there may be considerable variation in density and population structure on a smaller scale. The pattern of *C. stutchburyi* settlement indicated clumping of juveniles within a few m^2. Similarly, the gradient of adult density across the experimental area (Table 3.1) indicated a variation in density over an area of similar size. To

clarify this, a sampling programme was carried out, in one specific area, near the experimental plots, to assess the pattern of "microdistribution" of *C. stutchburyi*, to investigate population structure and to assess the effect of sample size on density estimates.

Twenty-five sites were located within a 2500 m^2 area of mudflat marked into a 5 × 5 grid of 100 m^2 squares according to a stratified random pattern. At each point, nine 0.025 m^2 quadrats were excavated as indicated in Fig. 3.4 to a depth of 50 mm; the *C. stutchburyi* were removed by sieving and retained.

North

E1	E2	E3	E4	E5
D1	D2	D3	D4	D5
C1	C2	C3	C4	C5
B1	B2	B3	B4	B5
A1	A2	A3	A4	A5

5	6	7
2	3	8
1	4	9

Fig. 3.4 Sample design of survey to test microdistribution of *C. stutchburyi*. Top, orientation of the grid of 100 m^2 squares. Bottom, orientation of the nine 0.025 m^2 quadrats taken within each square.

In examination of the microdistribution in this area, the null hypothesis; "that *C. stutchburyi* is distributed randomly" was tested using the following two techniques:

A) Comparison of density using the variance:mean ratio (from Kershaw, 1964), and

B) Comparison of density using a Chi square value calculated from the index of dispersion (from Pielou, 1969).

Distribution and density of adult (> 5 mm) and young-of-year (< 5 mm) *C. stutchburyi* was compared among the 25 sites, based upon nine sample sizes from 0.025 to 0.225 m^2 (Tables 3.6, 3.7).

Table 3.6 Analysis of the distribution of *C. stutchburyi* (> 5 mm shell length) at 25 sites, sampled with nine quadrat sizes.

Sample size (m^2)	.025	.050	.075	.100	.125	.150	.175	.200	.225
$\frac{S^2}{\bar{x}}$	3.3	3.7	5.1	11.4	9.1	9.1	8.9	8.5	10.1
value of t	7.8	9.4	14.3	36.3	27.9	28.0	27.3	25.9	31.5
χ^2	78.4	89.4	123.3	220.3	217.0	218.0	213.5	205.0	242.7

Table 3.7 Analysis of the distribution of young-of-year (< 5 mm shell length) *C. stutchburyi* at 25 sites, sampled with nine quadrat sizes.

Sample size (m^2)	.025	.050	.075	.100	.125	.150	.175	.200	.225
$\frac{S^2}{\bar{x}}$	1.7	2.8	2.5	6.1	7.7	5.2	7.0	7.8	7.5
value of t	2.5	6.1	5.0	17.5	23.1	14.6	20.8	23.5	22.6
χ^2	41.6	66.5	58.5	145.4	184.3	125.3	168.4	187.3	227.3

The variance:mean ratio in all cases shows some degree of contagion. When tested with the t test, the difference from the expected ratio (of 1) was significant at the 0.02 level for all quadrat sizes for both adult and juvenile distributions; and was significant at the 0.001 level in all cases except the smallest quadrat size for juveniles. It is therefore possible to reject the hypothesis that distribution is random among the 25 sites when investigated using samples of 0.025 to 0.225 m^2. Further, the variance:mean ratio was greater than one in all cases indicating that the distribution of cockles was aggregated, or clumped.

The results of the Chi squared test support the decision to reject the hypothesis as the departure from randomness was significant at the 0.025 level in the case of the smallest sample from the juvenile population, and at the 0.005 level in all other cases.

Analysis of the nine adjacent quadrats at each site (Table 3.8) reveals that animal numbers among the nine quadrats also showed a significant departure from randomness ($t < 0.2$, $\chi^2 < 0.1$) at 15 of the 25 sites. Even on this small scale, the variance:mean ratio indicated a clumped distribution in all significant cases, and in all other cases except one.

It appears from Table 3.9 that there was no general pattern to the distribution of density within the experimental area (based on a quadrat size of 0.1 m^2). Mean size was reasonably uniform (range 18.6 to 26.7 mm) and was independent of density.

The patchy nature of cockle distribution was confirmed by determining density using increasingly large samples. Accuracy of the density estimate improves with increasing quadrat size to 0.1 m^2 (Fig. 3.5) but does not improve beyond that.

Table 3.8 Analysis of the density of *C. stutchburyi* in nine adjacent samples at each of 25 sites.

	$\bar{x}$	$\frac{s^2}{\bar{x}}$	t	Level of significance	χ^2	Level of significance
A1	9.2	2.15	2.30	.1	17.20	.05
A2	11.3	4.09	6.17	.001	32.68	.005
A3	10.1	1.18	0.35	ns	9.40	ns
A4	6.4	1.02	0.004	ns	8.16	ns
A5	7.9	1.95	1.89	.1	15.57	.05
B1	13.2	2.25	2.50	.05	18.00	.025
B2	14.8	1.11	0.22	ns	8.89	ns
B3	11.7	1.24	0.47	ns	9.88	ns
B4	12.5	2.06	2.12	.1	16.50	.05
B5	8.1	1.40	0.81	ns	11.20	ns
C1	13.5	1.89	1.78	.2	15.13	.1
C2	18.4	3.51	5.01	.01	28.06	.005
C3	17.1	0.55	-0.90	ns	4.38	ns
C4	16.3	2.64	3.28	.02	21.10	.01
C5	17.2	2.21	2.41	.05	17.65	.025
D1	18.2	3.58	5.16	.001	28.66	.005
D2	14.2	2.94	3.87	.01	23.49	.005
D3	15.4	1.79	1.57	.2	14.30	.01
D4	13.3	1.94	1.87	.1	15.49	.01
D5	15.4	3.35	4.69	.01	26.77	.005
E1	10.3	1.33	0.67	ns	10.68	ns
E2	11.4	1.14	0.29	ns	9.14	ns
E3	17.4	1.22	0.45	ns	9.78	ns
E4	22.4	3.77	5.55	.001	30.19	.005
E5	19.0	1.11	0.21	ns	8.84	ns

Table 3.9 Distribution of density (number per quadrat of 0.1 m^2) and mean size (mm) of *C. stutchburyi* at 25 sites.

	1		2		3		4		5	
	Number	Size	Number	Size	Number	Size	Number	Size	Number	Size
E	37	21.2	44	22.1	60	23.1	114	23.4	85	20.3
D	62	25.7	54	21.9	56	18.6	51	21.3	60	22.7
C	58	22.4	79	23.5	77	23.0	62	20.1	73	22.1
B	39	23.1	47	23.4	46	22.5	46	22.7	28	23.1
A	23	26.7	48	20.4	40	23.1	24	20.8	32	20.3

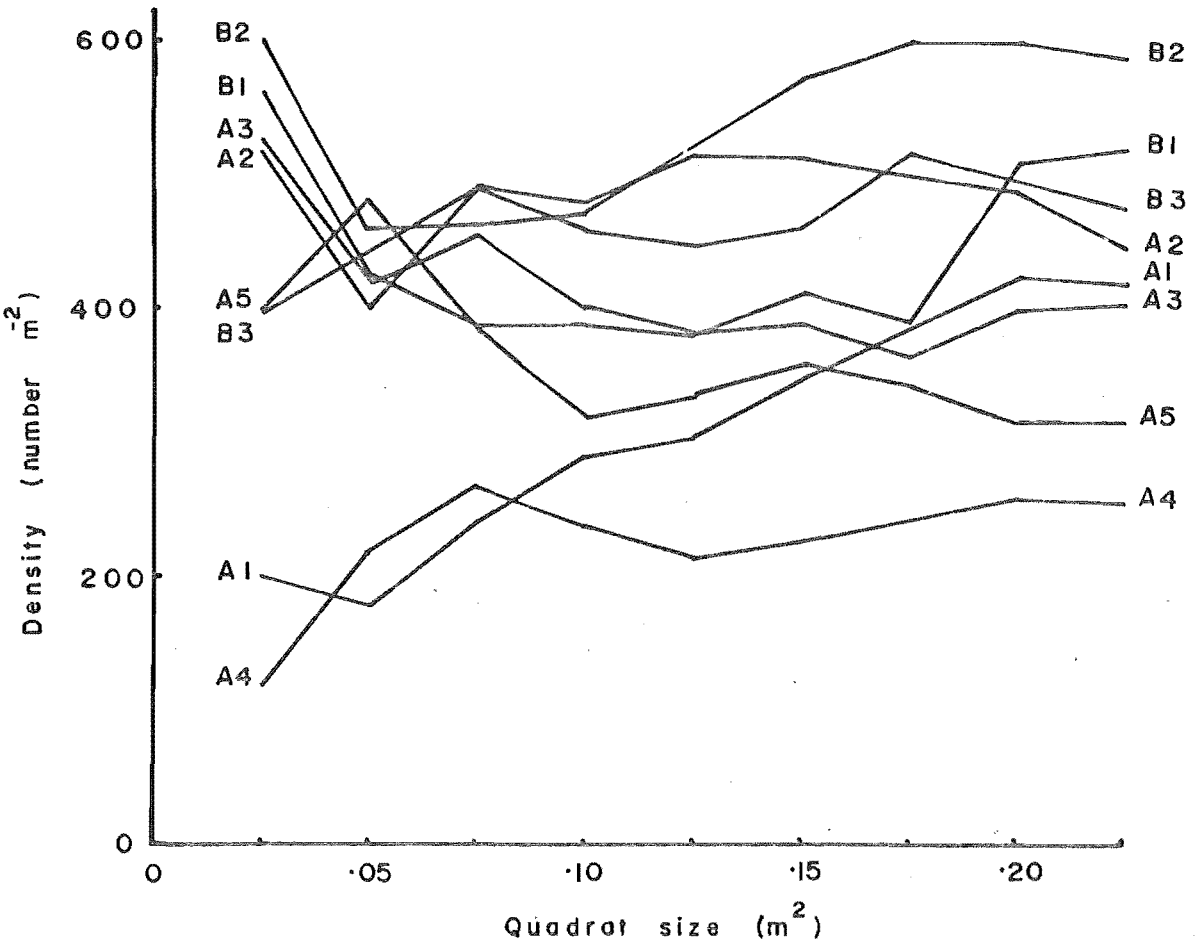


Fig. 3.5 Effect of increasing quadrat size on estimate of density of *C. stutchburyi* at eight sites in the Avon-Heathcote Estuary.

4 AN ENERGY BUDGET FOR *C. STUTCHBURYI*

4.1 INTRODUCTION

Energy flows through animal populations by way of food webs. In general, it is the organic matter produced by plants (from simple inorganic substances and the energy of the sun) that is ultimately decomposed into simple inorganic compounds by animals with the release of energy. Some of the complex organic matter is rearranged into tissue, other is used to fuel metabolic processes (and the energy dissipated as heat).

The mechanisms of food transformation by an animal or population may be represented by a schematic flow diagram as in Fig. 4.1 (Petrusewicz, 1967; Petrusewicz & Macfadyen, 1970); the various components of consumed food have different fates. Food may ultimately become biomass, or its energy used in respiration, or it may be egested.

Productivity studies have evolved partially out of interest in the quantities of animal matter that can be produced for subsequent utilisation in the food chain. They form a rather young branch of ecology (Petrusewicz & Macfadyen, 1970) but one which received considerable attention as the theme of the International Biological Programme.

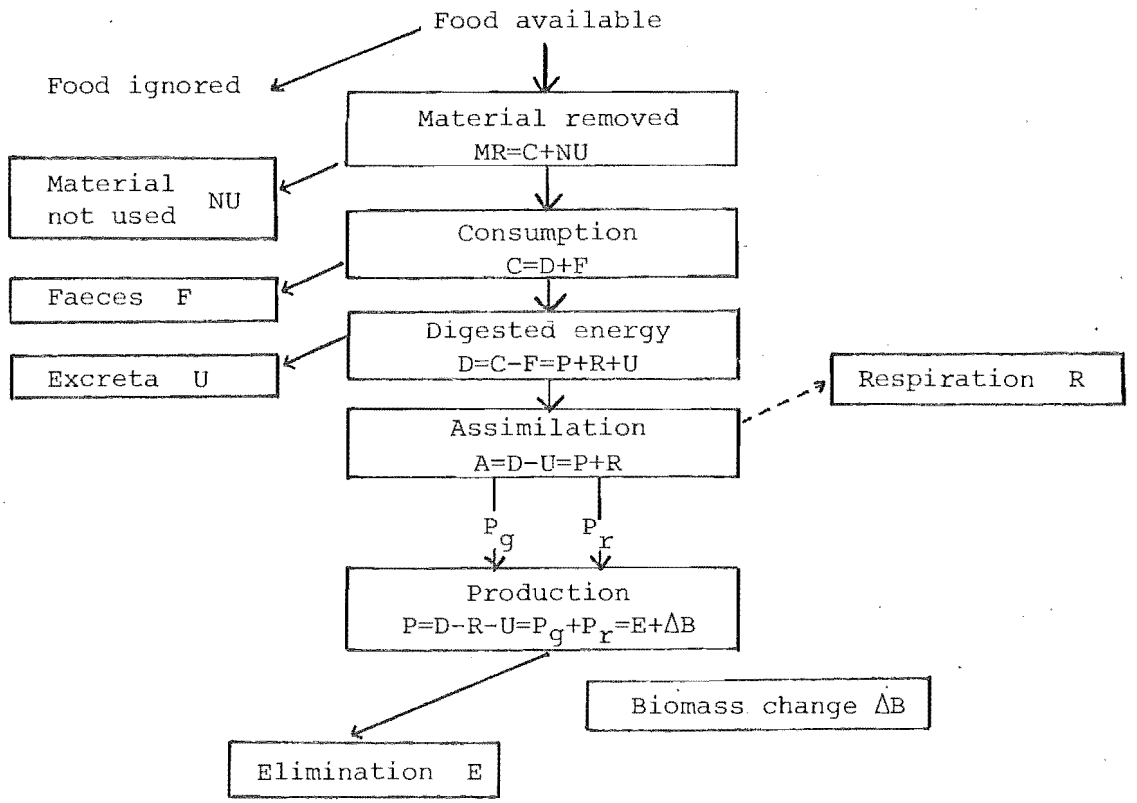
Although the transformation of food matter itself, or any essential component of food such as nutrients or carbon may be investigated in studies linking producers and consumers, energy forms the most common denominator for comparison. An energy budget relates the intake of food energy by an individual organism, a population or a community and its subsequent utilisation according to the equation:

$$C = P + R + F + U$$

where C = consumption, P = production, R = respirations, F = faeces and U = urine (Ricker, 1968; Grodzinski *et al.*, 1975) expressed in units of energy (calories or joules).

H.T. Odum (in press) presents a diagram of the main energy sources and outflows for a typical population of consumer units in which the influence of additional energy sources (such as recruitment and environmental parameters) are also considered. This model is presented with IBP terminology in Fig. 4.2

As a benthic dwelling, filter feeding mollusc, the functional components of an energy budget for individual *C. stutchburyi* may be represented as in Fig. 4.3.



MR total material removed by the population examined,

NU material removed but not used (not consumed),

C consumption,

FU rejecta,

F egesta,

U excreta,

A assimilation,

D digested energy (material),

P production,

P_g production due to body growth,

P_r production due to reproduction,

R respiration (cost of maintenance),

ΔB changes in biomass (standing crop) of population,

E elimination.

Fig. 4.1 Schematic diagram of energy flow through an animal or population (after Petrusewicz, 1967; Petrusewicz & Macfadyen, 1970).

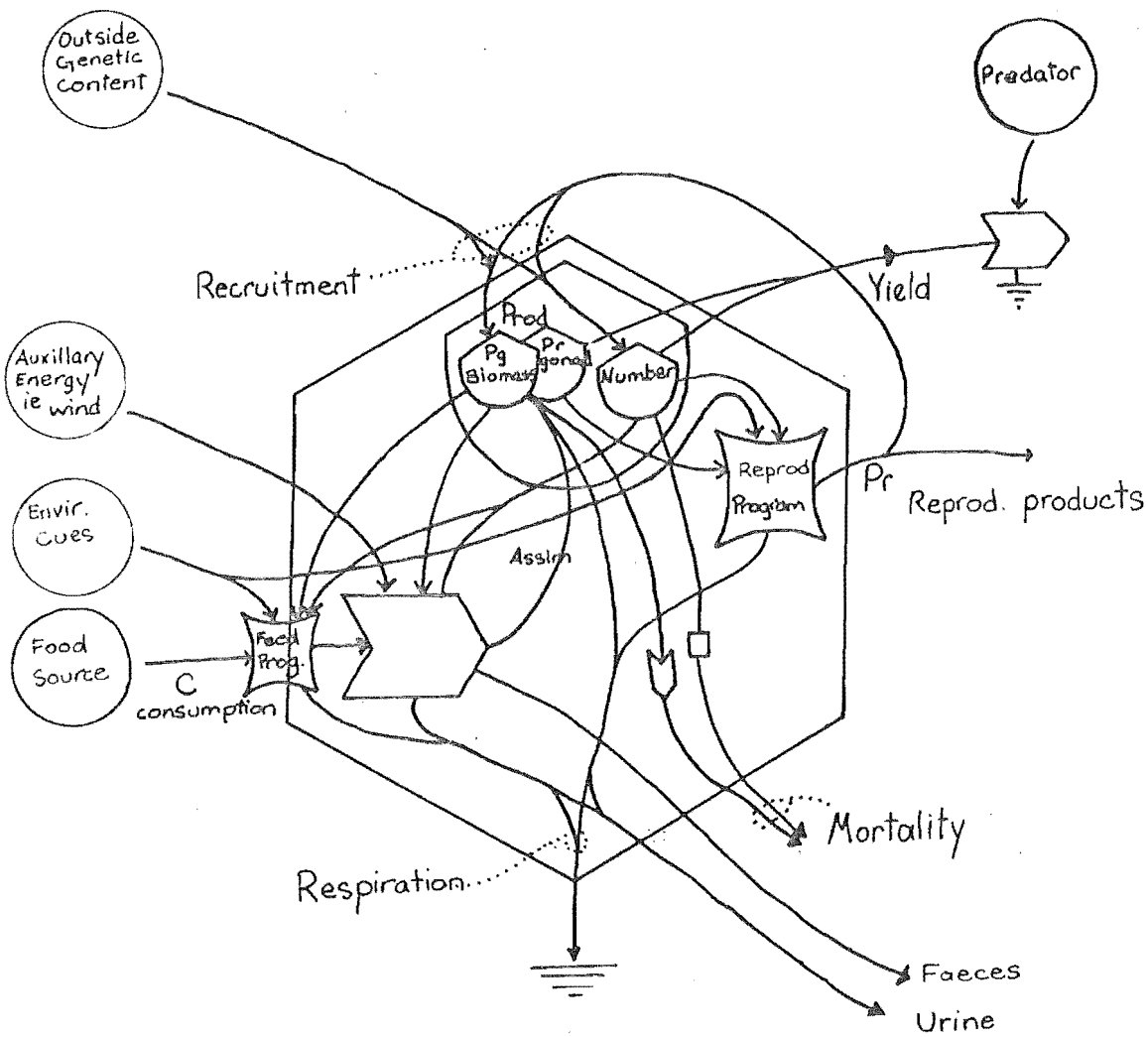


Fig. 4.2 Diagram of the major energy sources and flows for a typical population of consumer units (after H.T. Odum, in press) modified to include IBP energetic terminology. Symbols are explained in Fig. 5.1.

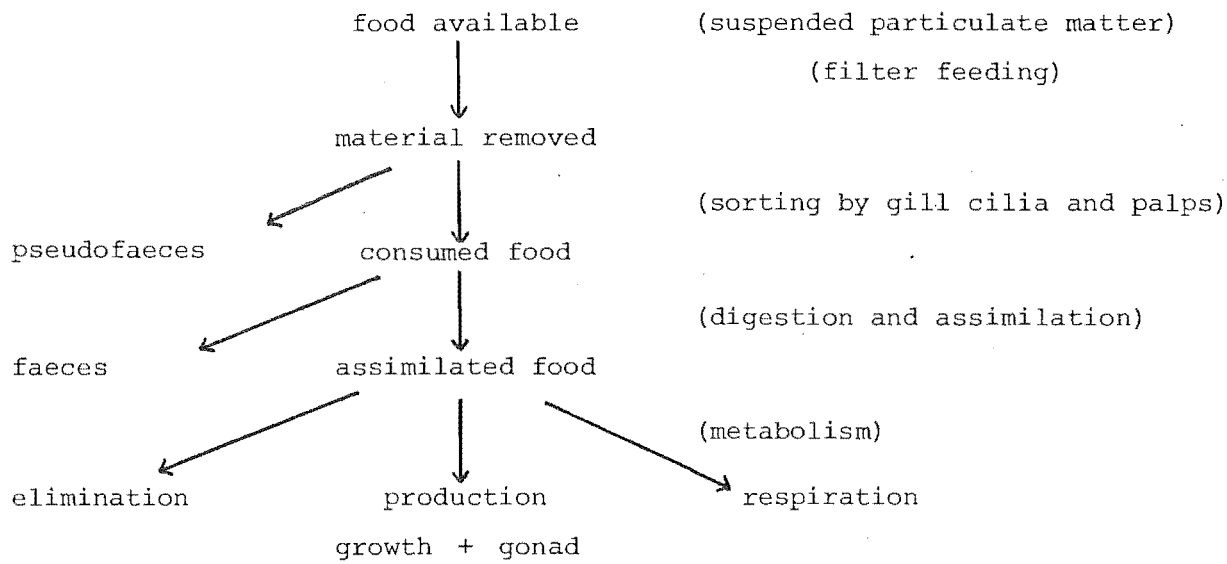
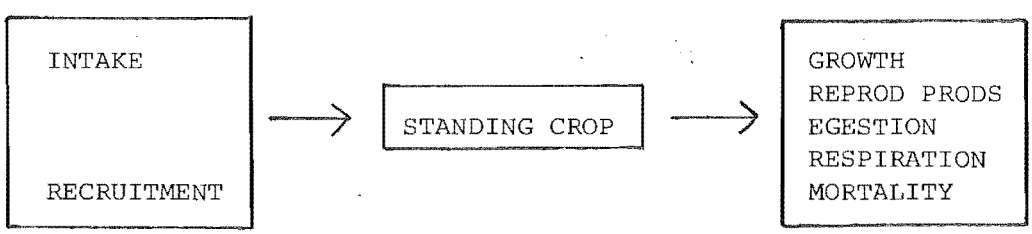


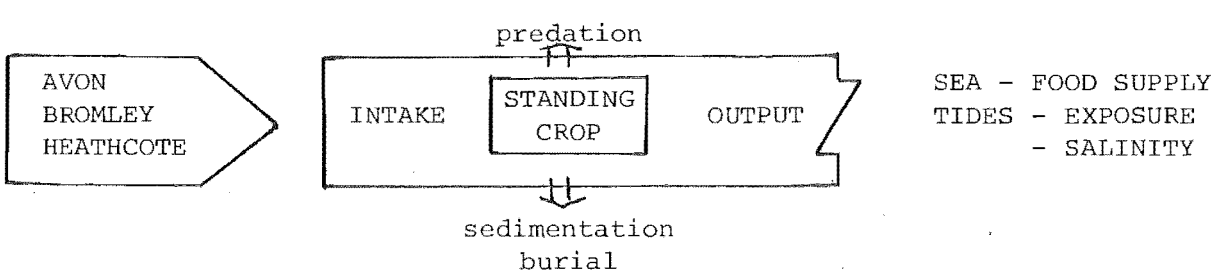
Fig. 4.3 Schematic diagram of the functional components of an energy budget for *C. stutchburyi*.

The energy flow through a population of *C. stutchburyi* may be compartmentalised



with inputs from food intake and recruitment reflecting a change in standing crop through the channels of growth, reproduction, egestion, respiration and mortality.

The above model may be inserted into a representation of the estuary as it relates to *Chione*;



In this section an energy budget is constructed for the *C. stutchburyi* population in the Avon-Heathcote Estuary. The parameters of an energy budget described above are considered in turn and values are estimated from both original work and literature results. A summary of the budget is presented in section 4.9.

4.2 ENERGY CONTENT OF *C. STUTCHBURYI*

Traditionally energy has been expressed in calories (cal) or kilocalories (kcal or Cal) in ecological studies and for convenience in comparing this study with others (e.g. Jansson & Zucchetto, 1978) I have chosen to use the kilojoule (kJ); 1 kcal = 4.187 kJ.

In studies of productivity and energy flow, transformations of energy between organisms or trophic levels are based on the amount of matter involved, multiplied by the calorific value of that matter. Calorific values have been measured (by bomb calorimetry), or calculated from the composition of the matter (the amount of carbohydrate, fat and protein multiplied by the appropriate calorific coefficient) and expressed in terms of the dry, ash-free dry or wet weight of the substance involved.

A great deal of calorific data exists in the literature (e.g. Golley, 1960, 1961; Cummins, 1967; Cummins & Wuycheck, 1971; Thayer *et al.*, 1973; Salonen *et al.*, 1976) and confidence in the precision of the technique is increasing due to methodological investigations such as those of Paine (1971), Elliott & Davison (1975) and Schroeder (1977).

Slobodkin & Richman (1961) observed that calorific values (per ash-free gram) do not vary greatly throughout the animal kingdom (5400 - 6100 cal/g or 22.6 - 25.5 kJ/g) and although recent studies have increased these limits in both directions, their general observation appears to hold.

A calorific study of the body components of *C. stutchburyi* was undertaken using a Parr 1411 combustion calorimeter. Flesh tissue (Table 4.1) ranged in calorific value from 18.07 kJ g^{-1} (mantle) to 21.36 kJ g^{-1} (digestive diverticulum) ash-free dry weight. Using the calorific value of each body component and the proportion of the total flesh weight represented (Table 4.1) a mean body dry tissue calorific value of 19.71 kJ g^{-1} was calculated.

The storage cycle in bivalves involves the accumulation of carbohydrate, mainly glycogen, in the adult and its conversion to lipid for storage in the ova. Glycogen represents an easily accessible store

of energy (via glucose) (Giess, 1966; Bayne, 1976) and its association with the digestive diverticulum explains the high calorific value of that tissue.

Table 4.1 Calorific values of the body components of *C. stutchburyi* (pooled tissues of ten individuals collected at Monck's Bay, March 1980).

Body component	% of dry flesh weight	% of total dry weight	Calorific value kJ g^{-1} *	n	range
gut and gonad	27.47	1.13	19.593	5	19.503 - 19.765
adductors	17.42	0.72	20.772	4	20.690 - 20.807
mantle	13.74	0.56	18.070	3	17.799 - 18.320
digestive gland	12.18	0.50	21.358	3	20.910 - 21.767
gills	11.69	0.48	19.043	3	18.846 - 19.274
siphons	9.40	0.39	18.501	3	18.208 - 18.758
foot	8.10	0.33	20.550	3	20.417 - 20.723
mean body dry tissue (calculated)	100		19.711		
gonad				1	19.995
shell and ligament		95.90			

* ash content of these tissues was considered to be negligible and in this case dry weight ≃ ash-free dry weight.

4.3 NET ORGANIC PRODUCTION

While the concept of production is usually understood to refer to the amount of biomass produced over a certain period of time, and therefore to be a measure of the bulk of matter contributed to succeeding stages of the food chain (Macfadyen, 1963), the methods of specific measurement and expression of production in the literature are numerous. Macfadyen (1948) noted confusion over the meaning of "productivity" and Petrusewicz & Macfadyen (1970) present five different definitions, "each of them characterizing different ecological views of the concept in question".

In its most general sense, "net production" may be considered to be the matter available to be utilised by the next stage of the food chain, divided by the time taken for that matter to be produced.

An estimate of the spatial distribution of "net production" of *C. stutchburyi* was made for the Avon-Heathcote Estuary as follows. Applying the length-age relationship (section 3.1) to the mean shell length of *C. stutchburyi* at each sample site, an estimate of mean age was obtained. Net production (gAFDWt m^{-2} yr^{-1}) was then estimated for each site (Fig. 4.4) as:

$$\frac{\text{accumulated organic biomass}}{\text{mean age of the population}}$$

The highest values of net production were about 15 gAFDWt m^{-2} yr^{-1}.

Net production as defined in this manner represents only accumulated organic matter and neglects that part of production which has gone into mortality, elimination, and reproduction (samples were taken in winter when the animals were in non-breeding condition). This is similar to the concept of "yield" of Petrusewicz & Macfadyen (1970) and represents the accumulated organic biomass of the system.

Estimates of the energy content of the cockle population were made on the basis of the biomass and net production data. Areas were measured from Figs 2.9 and 4.4 using a polar compensating planimeter, and estimated minimum and maximum values calculated for the energy in organic biomass (Table 4.2) and net production (Table 4.3) of each area. The total winter organic biomass of the Avon-Heathcote Estuary was estimated as being between 8.2×10^4 and 1.7×10^6 kg (ash-free dry weight), or 1.62×10^9 to 3.4×10^{10} kJ yr^{-1}.

4.4 SHELL AND FLESH PRODUCTION

Biomass production (body growth) (P_g) of bivalve molluscs has two aspects; flesh, which is primarily accumulated organic matter, and shell which has both an organic and inorganic fraction. Shell represents stored organic and inorganic matter which persists long after the death of the animal whereas flesh is primarily organic matter that may be easily transferred within the food chain, and quickly cycled on death of the animal.

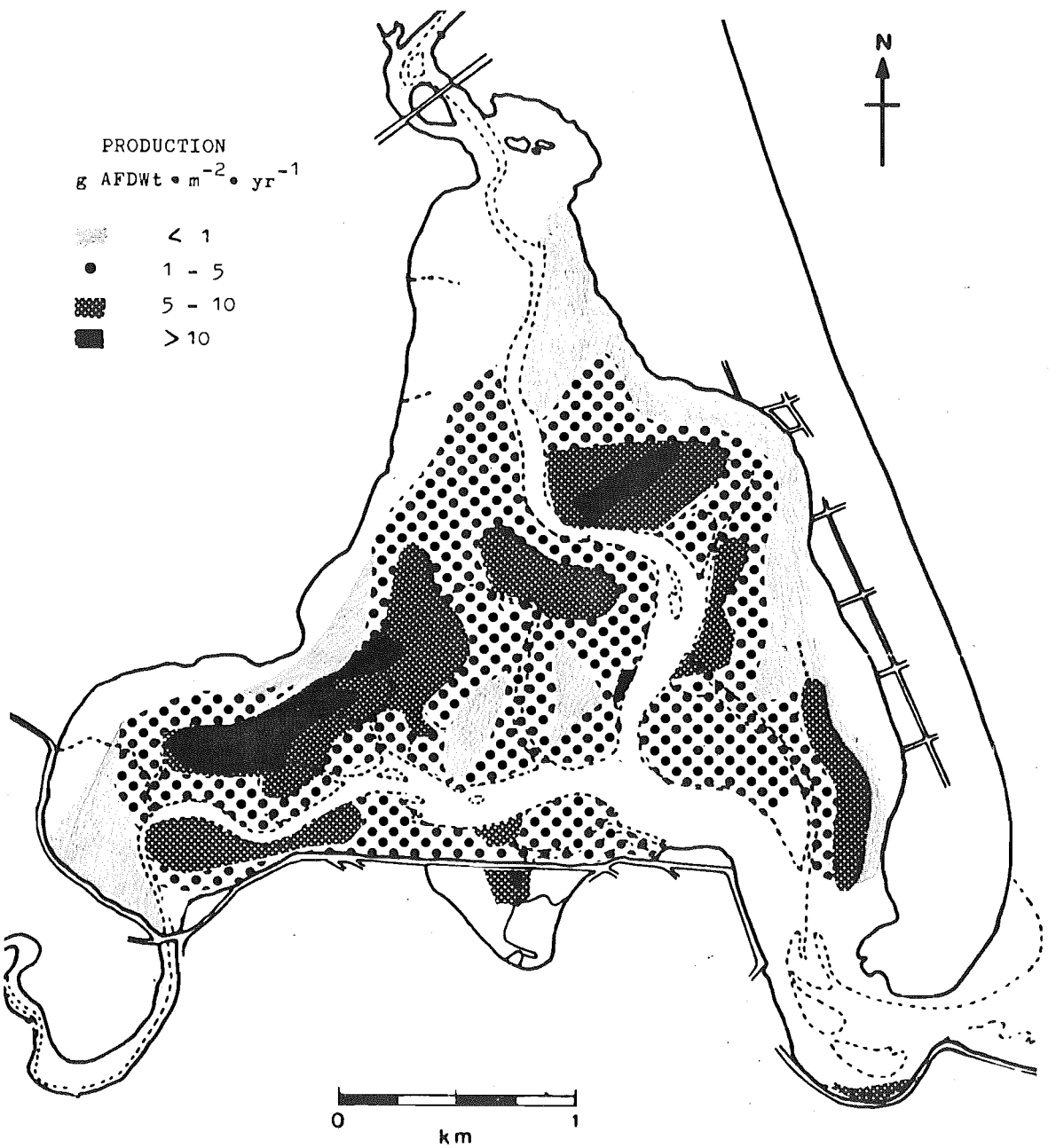


Fig. 4.4 Distribution of net production of *C. stutchburyi* in the Avon-Heathcote Estuary.

Table 4.2 Estimate of total winter *C. stutchburyi* biomass (g ash-free dry weight) and energy content (kJ) in the Avon-Heathcote Estuary; based upon distribution of biomass (Fig. 2.9) and on a mean tissue calorific value of 19.7 kJ g^{-1} (Table 4.1).

Biomass level ($g\ m^{-2}$)	Area (m^2)	Total biomass minimum $g\ m^{-2}$		g	maximum $g\ m^{-2}$		g
< 10	1.2×10^6	× 0	=	0	× 10	=	12×10^6
10 - 500	3.2×10^6	× 10	=	32×10^6	× 500	=	1600×10^6
> 500	0.1×10^6	× 500	=	50×10^6	× 1200	=	120×10^6
total ash-free dry winter biomass (g)		8.2×10^7			1.7×10^9		
total energy value (kJ)		1.62×10^9			3.4×10^{10}		

Table 4.3 Estimate of net production of *C. stutchburyi* in the Avon-Heathcote Estuary; calculated from the distribution of production (Fig. 4.4) and a mean tissue calorific value of 19.7 kJ g^{-1} (Table 4.1).

Production level ($g\ m^{-2}\ yr^{-1}$)	Area (m^2)	Total net production minimum $g\ m^{-2}\ yr^{-1}$		$g\ yr^{-1}$	maximum $g\ m^{-2}\ yr^{-1}$		$g\ yr^{-1}$
0 - 1	0.9×10^6	× 0	=	0	× 1	=	0.9×10^6
1 - 5	2.3×10^6	× 1	=	2.3×10^6	× 5	=	11.5×10^6
5 - 10	0.9×10^6	× 5	=	4.5×10^6	× 10	=	45.0×10^6
> 10	0.3×10^6	× 10	=	3.0×10^6	× 15	=	4.5×10^6
Total yearly net production (gAFDWt yr^{-1})		9.8×10^6			6.19×10^7		
Total energy produced (kJ yr^{-1})		1.93×10^8			1.2×10^9		

The relationships between wet, dry and ash-free dry weights of flesh and shell were determined for the animals used in the investigation of shell morphology (section 2.2.3).

Mean water content (loss on drying, based upon 375 individuals) was approximately 4% of shell wet weight (Table 4.4 A). It was almost identical for all shells examined, and the proportion did not change appreciably with increasing shell size (weight) (Fig. 4.5). Water content accounted for approximately 87.6% of flesh weight (Table 4.4 F) and the regression of dry flesh on wet flesh was linear (Fig. 4.6). Ash-free dry weight of shell was 8% of dry shell (Table 4.4 C) and 5% of wet shell weight (Table 4.4 B). There was considerable variability in both cases (Figs 4.7, 4.8) and there is a discrepancy of 2.7% between the value of AFS/WS calculated from measurements and that predicted by other ratios. Ash-free dry weight of flesh accounted for 77% of the dry flesh (Table 4.4 H, Fig. 4.9) and 10% of the wet flesh weight (Table 4.4 G, Fig. 4.10). Ash-free dry shell weight accounted for 61% of the total ash-free weight and flesh for the remaining 38% (Table 4.4 D and I, Figs 4.11 and 4.12).

Dry shell weight was approximately 12 times greater than that of total ash-free weight (Table 4.4 E) and dry flesh approximately 0.5 that of total ash-free dry weight (Table 4.4 J).

Ash-free shell and ash-free flesh weight (Fig. 4.13, Table 4.4 K) did not show as close a correlation (correlation coeff. = 0.68), and the ratio between the two had a relatively large standard error (AFS/AFF = 2.75, S.E. = .128, n = 998).

Approximately 61% of the total ash-free dry weight was shell organic matter (Table 4.4 D) and as this accounted for 8% of the total dry shell weight (Table 4.4 C), inorganic production (mostly $CaCO_3$) was estimated to be $0.61/8 \times 92 = 7.0$ g $gTAF^{-1}$. At production values estimated in section 4.3 of 9.8×10^6 to 61.9×10^6 $gAFDWt\ yr^{-1}$ (Table 4.3) the inorganic production due to shell accumulation was estimated at approximately 6.9×10^7 to 4.3×10^8 g dry inorganic matter per year.

The proportions of shell and flesh weights observed in this study are consistent with literature values for other bivalve molluscs. Price *et al.* (1976) reported shell and flesh weights for a variety of pelecypods (including *Chione cancellata* and *Mercenaria mercenaria* (Table 4.5)). Although all values for *C. stutchburyi* lie within the range established

Table 4.4 Regression equations and ratios describing shell and flesh weight parameters of *C. stutchburyi* from the Avon-Heathcote Estuary.

	Equation					r	r^2	ratio		S.E.	n	Fig.
A	dry shell	= 0.95	wet shell	-0.03		0.99	0.98	DS/WS	.96	.005	375	4.5
B	ash free shell	= 0.03	wet shell	+0.59		0.64	0.41	AFS/WS	.05	.003	355	4.7
C	ash free shell	= 0.03	dry shell	+0.05		0.70	0.49	AFS/DS	.08	.003	994	4.8
D	total ash free	= 1.53	ash free shell	+0.01		0.95	0.90	AFS/TAF	.61	.006	998	4.11
E								DS/TAF	12.38	.205	998	
F	dry flesh	= 0.13	wet flesh	-0.002		0.98	0.96	DF/WF	.12	.002	589	4.6
G	ash free flesh	= 0.10	wet flesh	-1.8×10^{-4}		0.96	0.92	AFF/WF	.10	.002	588	4.10
H	ash free flesh	= 0.72	dry flesh	-1.7×10^{-4}		0.97	0.94	AFF/DF	.77	.004	989	4.9
I	total ash free	= 2.19	ash free flesh	+0.04		0.87	0.76	AFF/TAF	.38	.006	998	4.12
J								DF/TAF	.53	.021	998	
K	ash free shell	= 1.19	ash free flesh	+0.04		0.68	0.46	AFS/AFF	2.75	.128	998	4.13

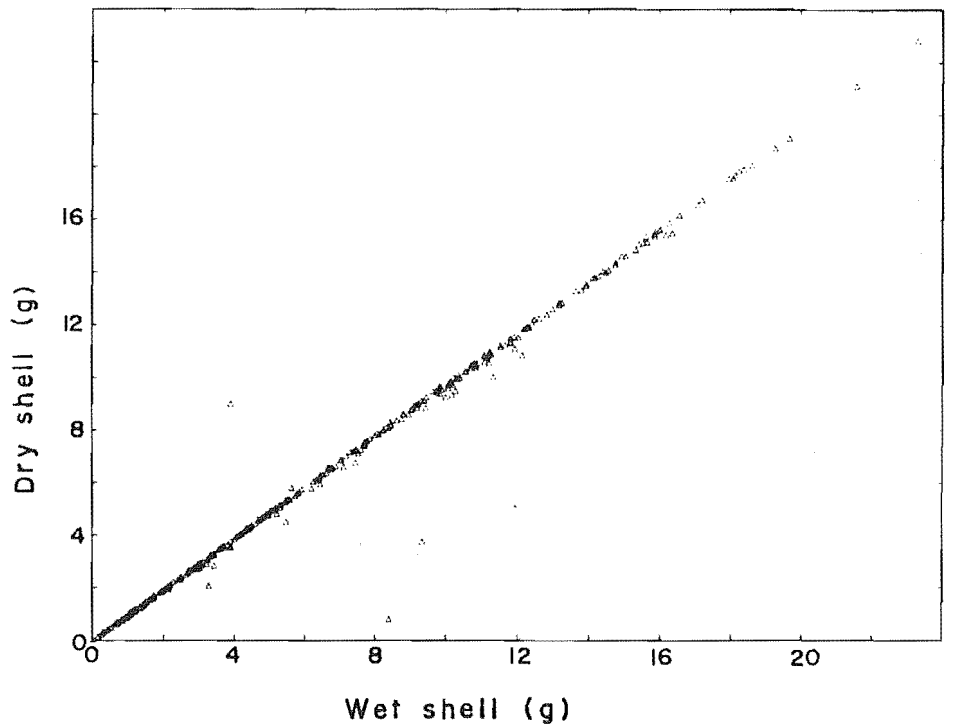


Fig. 4.5 Plot of wet shell weight against dry shell weight of individual *C. stutchburyi* (n = 375).

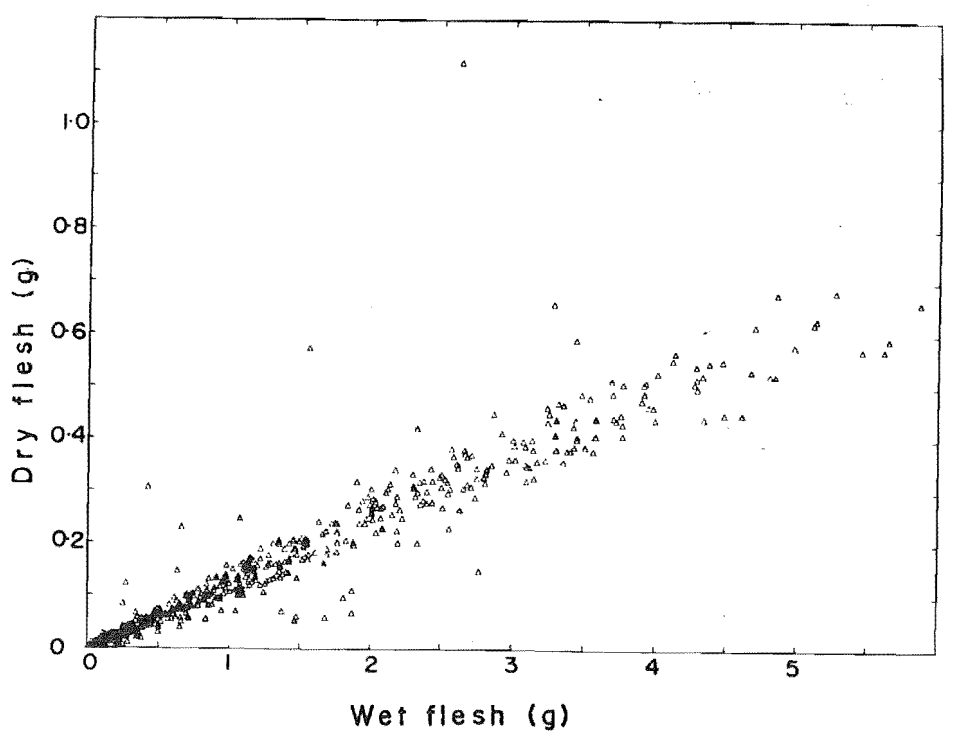


Fig. 4.6 Plot of wet flesh weight against dry flesh weight of individual *C. stutchburyi* (n = 589).

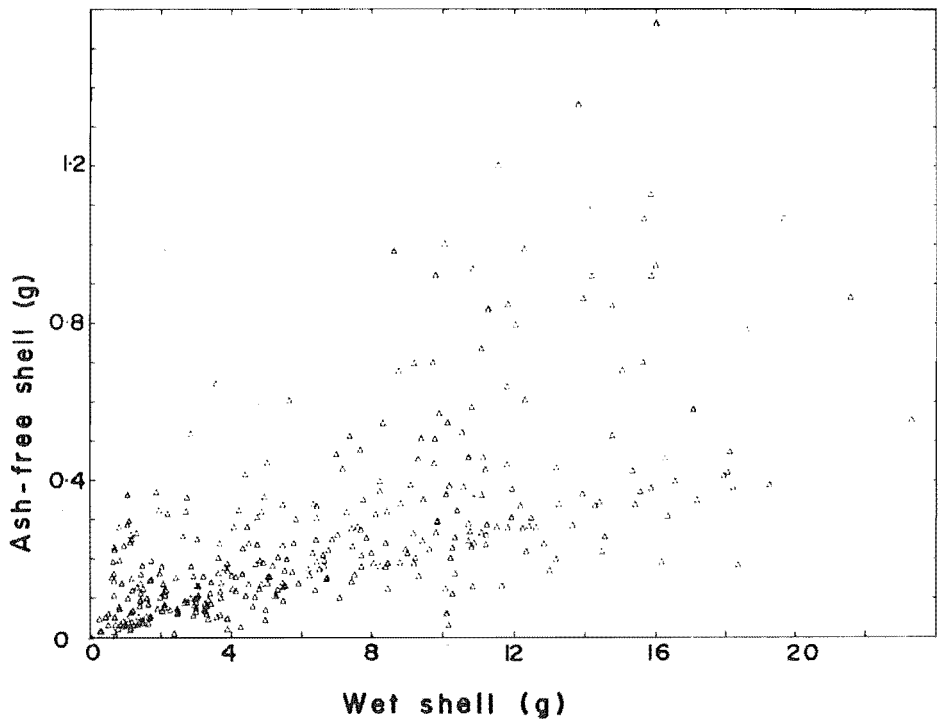


Fig. 4.7 Plot of wet shell weight against ash-free dry shell weight of individual *C. stutchburyi* (n = 355).

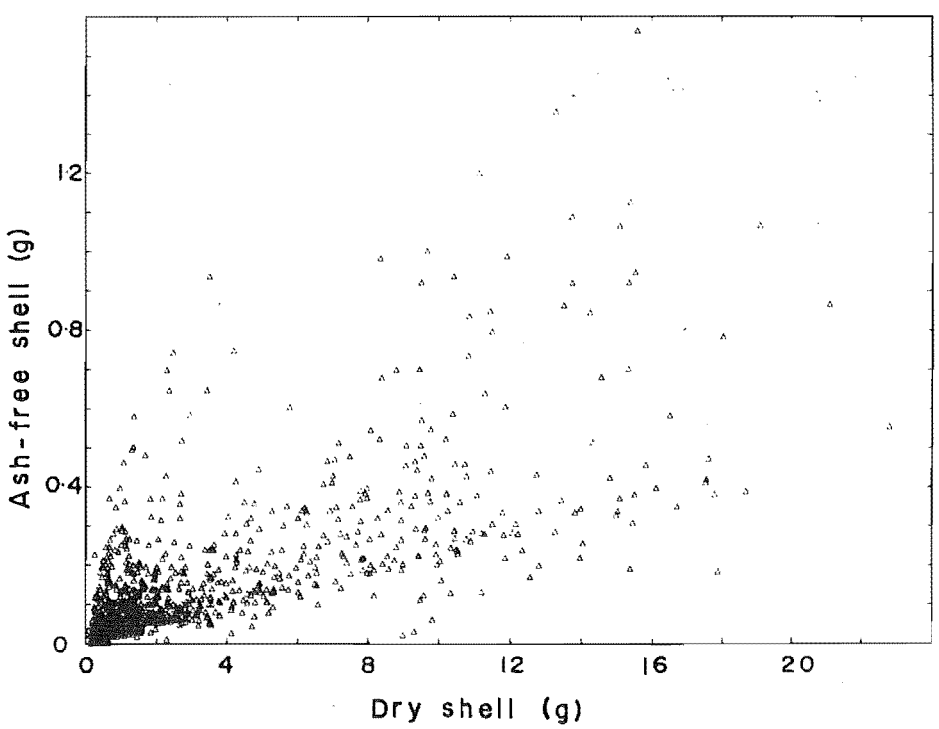


Fig. 4.8 Plot of dry shell weight against ash-free dry shell weight of individual *C. stutchburyi* (n = 994).

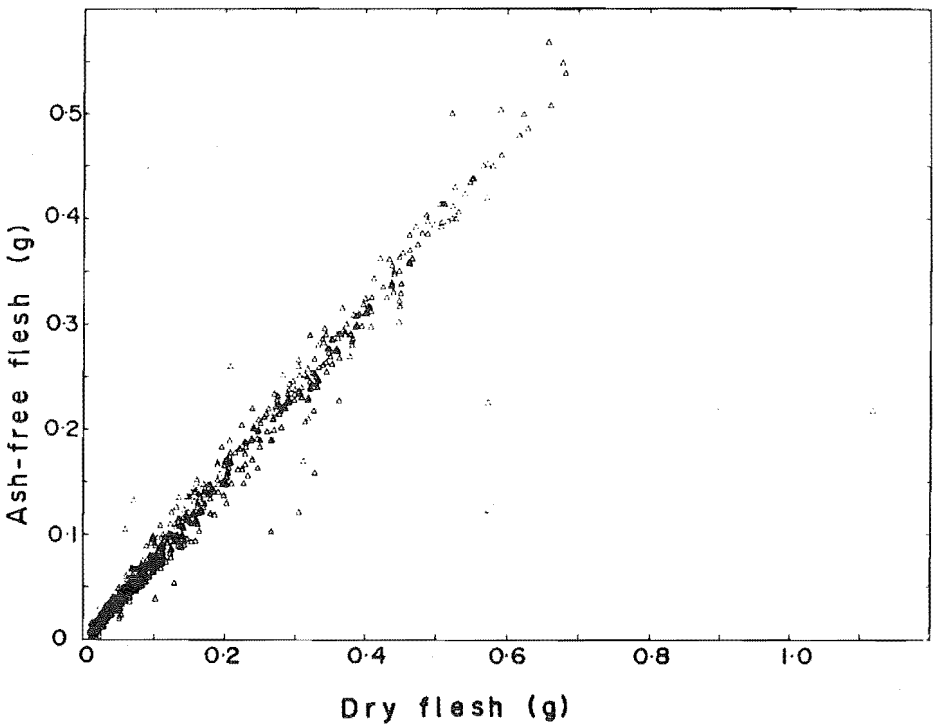


Fig. 4.9 Plot of dry flesh weight against ash-free dry flesh weight of individual *C. stutchburyi* (n = 989).

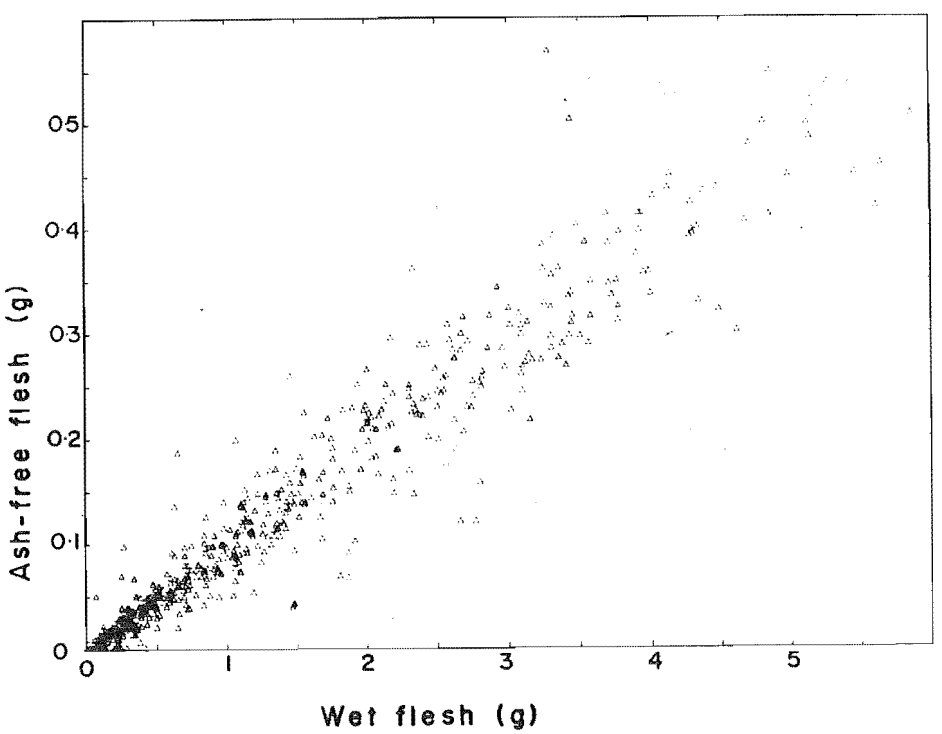


Fig. 4.10 Plot of wet flesh weight against ash-free dry flesh weight of individual *C. stutchburyi* (n = 588).

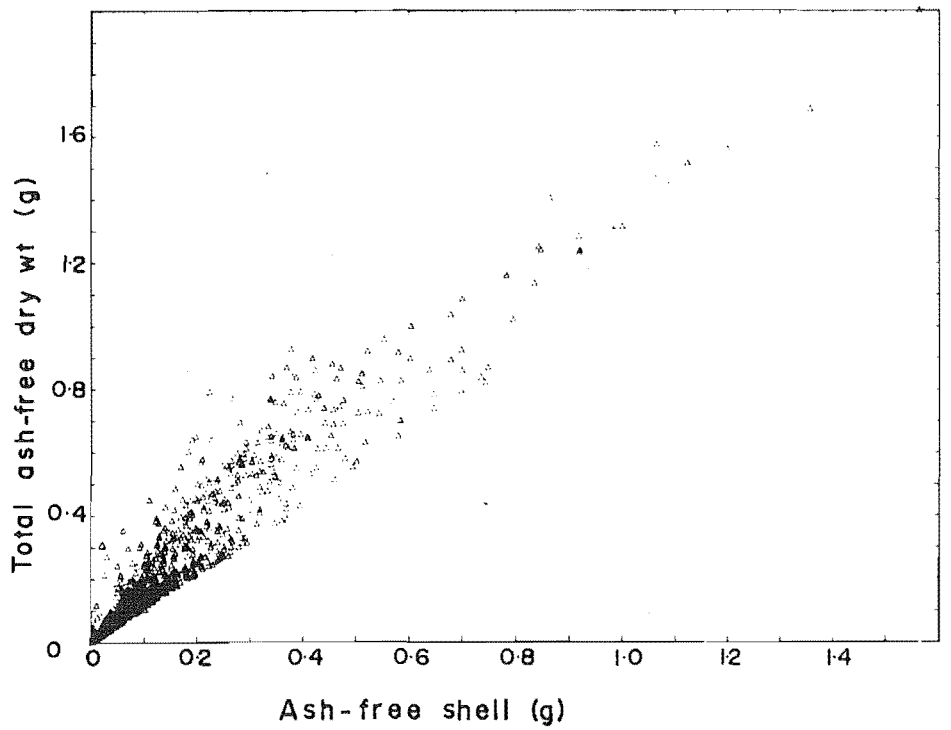


Fig. 4.11 Plot of ash-free dry shell weight against total ash-free dry weight of individual *C. stutchburyi* (n = 998).

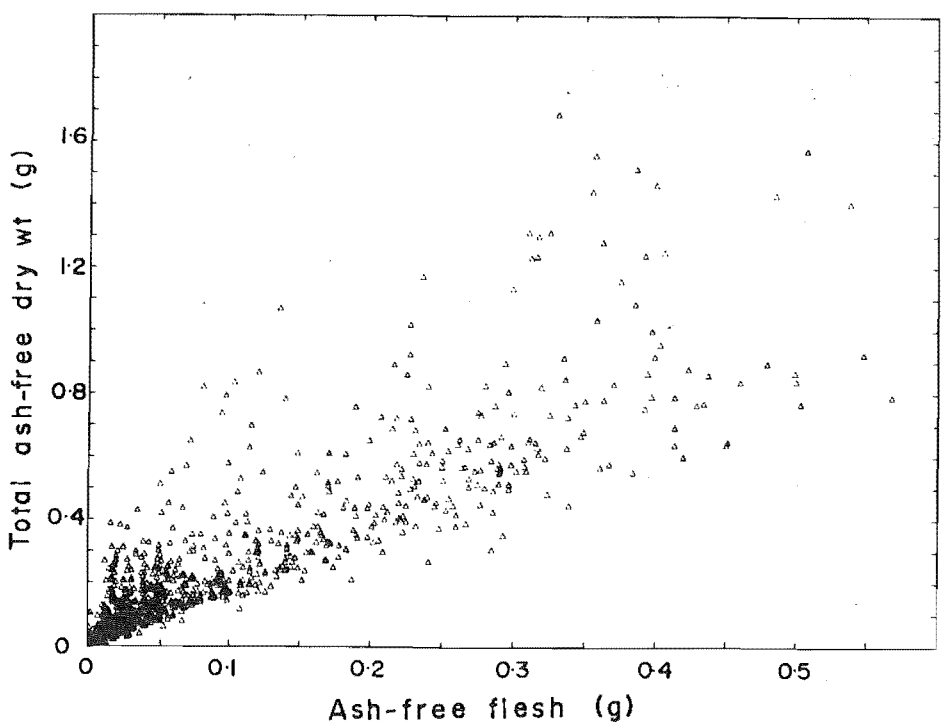


Fig. 4.12 Plot of ash-free dry flesh weight against total ash-free dry weight of individual *C. stutchburyi* (n = 998).

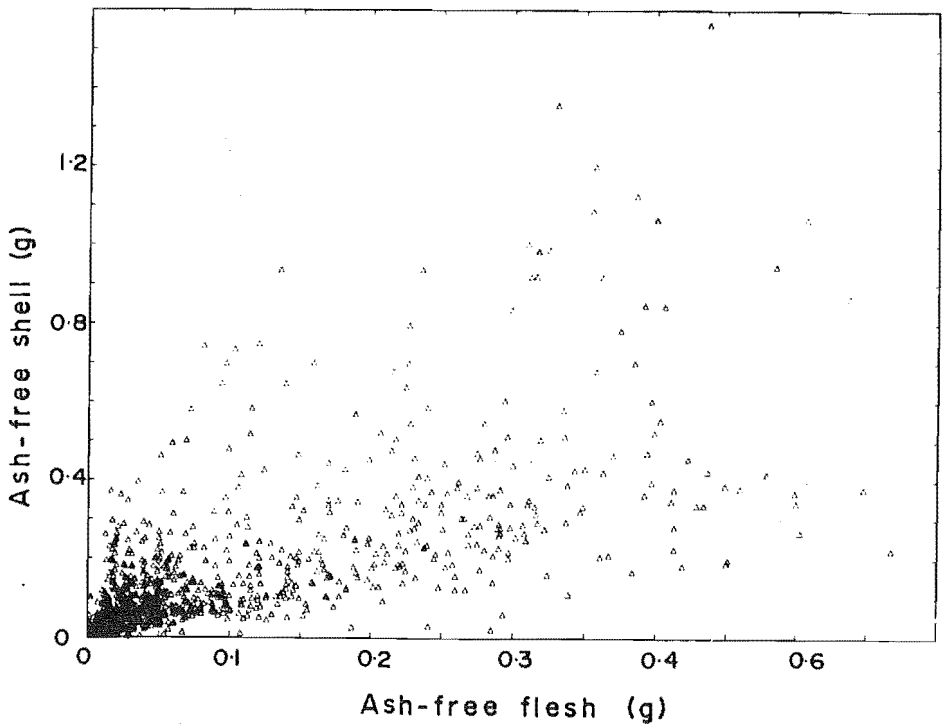


Fig. 4.13 Plot of ash-free dry flesh weight against ash-free dry shell weight of individual *C. stutchburyi* (n = 998).

for pelecypods, percent organic matter of shell (AFS/DS) appears higher in *C. stutchburyi* than average and results in a greater than average contribution of shell organic matter to the total (AFS/TAF).

Table 4.5 Comparison of the observed proportions of flesh and shell of *C. stutchburyi* with individual and mean values reported by Price *et al.* (1976) for other pelecypods.

Species	% ash-free dry weight shell AFS/DS	% ash-free dry weight flesh AFF/DF	% total organic matter shell AFS/TAF	% total organic matter flesh AFF/TAF
C. stutchburyi	8	77	61	38
C. cancellata	3.0 ± 0.8	79.4 ± 4.2	46.7 ± 7.6	49.4 ± 7.3
Mercenaria mercenaria	1.9 ± 0.2	79.8 ± 4.3	38.6 ± 3.8	54.3 ± 5.3
Range of pelecypods	1.4 - 21.4	67.2 - 93.9	12 - 71.9	25.5 - 87
Mean	4.3	80.9	35.4	62.3

Price *et al.* (1976) found that the contribution made by flesh and shell components to the total organic content was related to size; the contribution of the shell tending to increase with size. This is slightly apparent in *C. stutchburyi* where ash-free shell accounted for 61.3% of total ash-free dry weight of an animal of 0.1 g (ash-free shell) but 64.9% at an ash-free dry shell weight of 1.0 g (Table 4.4 D).

The division of *C. stutchburyi* organic matter between flesh and shell means a great difference in its subsequent use in the food chain. Only that organic matter in flesh (38% of the total) is readily available to the next trophic level (7.3×10^7 to 4.6×10^8 kJ yr^{-1}) and the remainder is slowly lost from shells during decomposition. Decomposition of bivalve shells is slow. Price *et al.* (1976) analysed oyster shells that had been weathered (unburied in an intertidal area) for at least 50 years and found them to contain 40% of the organic content of fresh shells, while Smith & Wright (1962) reported an organic content of 0.06% in weathered oyster shells dredged from the Gulf of Mexico. Clearly, cases of permanent burial of shells, a common occurrence in estuarine areas, may represent a significant sink of total organic biomass from the ecosystem.

4.5 REPRODUCTION

Sexes are separate in *C. stutchburyi* and the sex ratio is nearly 1:1 (Larcombe, 1971; Stephenson, unpubl. data). Larcombe (1971) reported that gonad development takes place only in individuals greater than 18 - 20 mm shell length, irrespective of age (in populations from Auckland to Dunedin). This was confirmed in the Avon-Heathcote Estuary, and suggests that reproduction is limited to individuals greater than two years of age (Fig. 3.1).

Gonad condition was measured during attempts to rear larvae, and qualitative estimates of "condition" based upon schemes of Moore & Lopez (1969), Boyden (1971), Larcombe (1971), and Kennedy (1977) were made. Ripe gonads were identified in males by full follicles that were even in colour, and by large sperm that were active on contact with sea water. Ripe females had follicles packed with eggs, often so dense that egg walls were angular and the foot distended.

C. stutchburyi had one breeding season per year. Gonad development began in September and the proportion of "ripe" individuals increased

until January. Spawning took place over a protracted late summer season (January - May) and individuals that had spawned were characterised by gonads that appeared ripe, but which were less densely packed and which contained broken cell wall fragments. Larcombe (1971) noted a similar pattern in all other populations that he studied, with peak spawning in January. Although apparently "ripe" gonads were noted before January, spawning could not be induced in individuals from Wellington Harbour (Stephenson & Chanley, 1979) nor fertilisation induced in dissected eggs from Avon-Heathcote Estuary populations before January.

Larcombe (1971) found that gonad production of *C. stutchburyi* averaged between 40% and 50% of the winter standing crop for adults with a mean length greater than 30 mm; but that in slow growing populations production was less, and that in cases in which *C. stutchburyi* did not reach a length of 20 mm no gonad was produced at all. In general, populations of *C. stutchburyi* that attain a total length of less than 20 mm will not contribute to the reproductive effort while those over 30 mm contribute approximately 40% of their winter dry flesh weight per year.

At a calorific value of 20.00 kJ g^{-1} for "pure gonad" (Table 4.1), the energy content involved in reproduction is estimated to be 20.00×0.4 B kJ m^{-2} yr^{-1} where B is the winter dry flesh biomass (Fig. 2.8). At the range of winter biomass estimated in Table 4.2 (8.2×10^7 - 1.7×10^9 g) the energy involved in reproduction of *C. stutchburyi* in the Avon-Heathcote Estuary is between 6.6×10^8 and 1.4×10^{10} kJ yr^{-1}.

Hughes (1970) shows that production of spawn in *Scrobicularia plana* ranged from 35% to 22% (of the winter standing crop) in low tide and high tide populations respectively. Moore & Lopez (1969) reported that half of the annual production of *C. cancellata* was gonad, and that weight loss due to spawning each year was about 43%. Bayne (1976) in a summary of much of the bivalve literature reported that mean calorific expenditure in gamete production as a proportion of the total production is 39%. These high values for gamete production in bivalves are consistent with a planktotrophic "strategy" (Vance, 1973a, 1973b) which is characterised by a high fecundity and a high metabolic cost (Bayne, 1976).

For some species, all of the energy available for production, once the demands of maintenance have been met, is eventually utilised in

gametogenesis; these species have no somatic growth once they are adult (Bayne, 1976) (for example, *Macoma balthica* in Massachusetts; Gilbert, 1973). Bayne (1976) discusses the seasonal variation of cycles of metabolic activity, gametogenesis, and nutrient storage and cited unpublished studies by Newell which show that *Cardium* demonstrates synchronous cycles of carbohydrate accumulation and gametogenesis, whereas others (*Mytilus* and *Donax*) seem to have these cycles out of phase. *C. stutchburyi* is likely to be of the *Cardium* type as it does not increase in body weight in winter, and Larcombe (1971) noted no detectable seasonal variation in calorific value of whole cockles which would indicate accumulation or utilisation of storage products. The spring and summer flesh weight increase of 30 - 50% of winter dry weight (Larcombe, 1971) represents the combined cycles of gametogenesis and nutrient storage as gonad.

4.6 RESPIRATION

Respiration (R) is a measure of the amount of assimilated energy utilised in maintenance activities (Petrusewicz & Macfadyen, 1970). It was not measured in this study, but an estimate was made from literature values.

The relationship between body size (usually weight) and the rate of respiration has been investigated for many animals including bivalves (see reviews by Brody, 1945; Kleiber, 1961; Zeuthen, 1953; Von Bertalanffy, 1957) and is usually described by the exponential equation;

$$R = aW^b$$

or logarithmically

$$\log R = \log a + b \log W,$$

where R = rate of oxygen consumption and W is the body weight.

Several researchers have attempted to define the variability to be expected in the slope (b) and several studies including those of Read (1962, on *Mytilus edulis* and *Modiolus demissus*), Pamatmat (1969, on *Transennella*) and Ansell (1973, on *Donax*) indicate that there is no significant variation in the value of b over a range of temperatures, at different levels of ration or at different times of the year. A common value of b = 0.703 was found by Ansell (1973) for 16 species of bivalve in Scottish waters.

However, the value of "a" (which is equivalent to the respiration rate per unit body size) is variable, and changes in response to environmental conditions such as ration, temperature, exposure, salinity, etc. (Bayne *et al.*, 1976). This has caused debate over the accuracy of respiration rates measured under unnatural conditions (in several types of respirometers) and the applicability of measured respiration rates to energy budgets. Wightman (1977, pers. comm.) for example compared oxygen consumption of terrestrial insects measured by a variety of respirometric techniques, and calculated from the energy budget equation; and found measured values to be less than half those obtained by calculation.

The rate of oxygen consumption has been found to vary with change in virtually any environmental variable as well as with physiological state of the animal concerned (Bayne *et al.*, 1976), and a wealth of literature exists on this topic. However, enough data has been published on respiration rates of bivalves under a variety of conditions and using a variety of respirometric techniques to allow an estimate of R to be made for *C. stutchburyi*.

Assuming an approximate metabolic rate of 8 J g^{-1} hr^{-1}, the energy expended in respiration by *C. stutchburyi* is estimated as 7.1 kJ g^{-1} yr^{-1}; and from the total population 5.8×10^{8} to 1.2×10^{10} kJ yr^{-1}.

Newell & Bayne (1980) noted seasonal cycles in the rate of oxygen consumption by *Cardium (=Cerastoderma) edule*. Using the oxycalorific coefficient of 20.098 J ml^{-1} O_2 (Pamatmat, 1978), the seasonal range in respired energy of their animals is estimated to be between 7.03 and 17.89 (mean = 11.25) J g(dry flesh)$^{-1}$ hr^{-1} (Table 4.6).

Table 4.6 Respiration rate (from Newell & Bayne, 1980) and calculated energy loss of *Cardium edule* based upon the oxycalorific coefficient of 20.098 J ml^{-1} O_2 (Pamatmat, 1978).

Season	O_2 consumption (ml O_2 g^{-1} hr^{-1})	Energy loss (J g^{-1} hr^{-1})
Minimum (March)	0.35	7.03
Maximum (April/May)	0.89	17.89
Mean	0.56	11.25

The behaviour of shell gaping leading to aerial respiration noted by Boyden (1972a, 1972b) in *Cerastoderma edule* was not noted in *C. stutchburyi* under natural conditions, although animals kept out of water for several tide cycles did exhibit periods of shell gaping and valve activity of this sort. Aerial respiration is not considered to be significant in this species *in situ*.

Pamatmat (1979) measured anaerobic metabolism in several estuarine bivalves including *Cardium edule* and calculated the regression equation for anaerobic metabolism at 20°C;

$$Y = 0.089 \times 10^{-4} + 1.58 \times 10^{-4} X \quad (r^2 = 0.83, 29 \text{ DF})$$

where Y = rate of heat production (J sec^{-1}) and X = dry tissue weight (g). Anaerobic heat production of the mussel *(Modiolus demissus)* was recorded as 0.58 J g^{-1} hr^{-1}; and was calculated to be 7.5% of the value of aerobic metabolism (7.63 J g^{-1} hr^{-1}).

Hammen (1979) compared the oxygen consumption rate (Q_O) measured with standard manometric equipment, with heat production (Q_H) and found that the ratio Q_H/Q_O ranged from 0.46 (*Mya arenaria*) to 3.40 (*Crassostrea virginica*). The former result is very near the extreme values for complete oxidation of foodstuffs (e.g. 0.432 J μ $mole^{-1}$ for complete oxidation of alanine etc.) and the latter result is interpreted as indicating an underestimate of Q_O (oxygen consumption) (Hammen, 1979). Hammen (1979) suggests that heat production (Q_H) measured by direct calorimetry is a more accurate representation of metabolism; and ranged from 1.59 - 6.23 J hr^{-1} g^{-1} (wet) tissue for four species of bivalve *(Mytilus edulis, Crassostrea virginica, Mya arenaria* and *Mercenaria mercenaria)*. Assuming dry weight to be less than 20% of wet weight, the range of metabolic heat production calculated from these values was estimated to be 8 to 31 J hr^{-1} g^{-1} dry tissue.

4.7 MORTALITY

C. stutchburyi is a reasonably long lived species, attaining an age of more than 20 years in some populations (section 3). Although there appear to be a wide variety of causes of mortality, three seem to be most important.

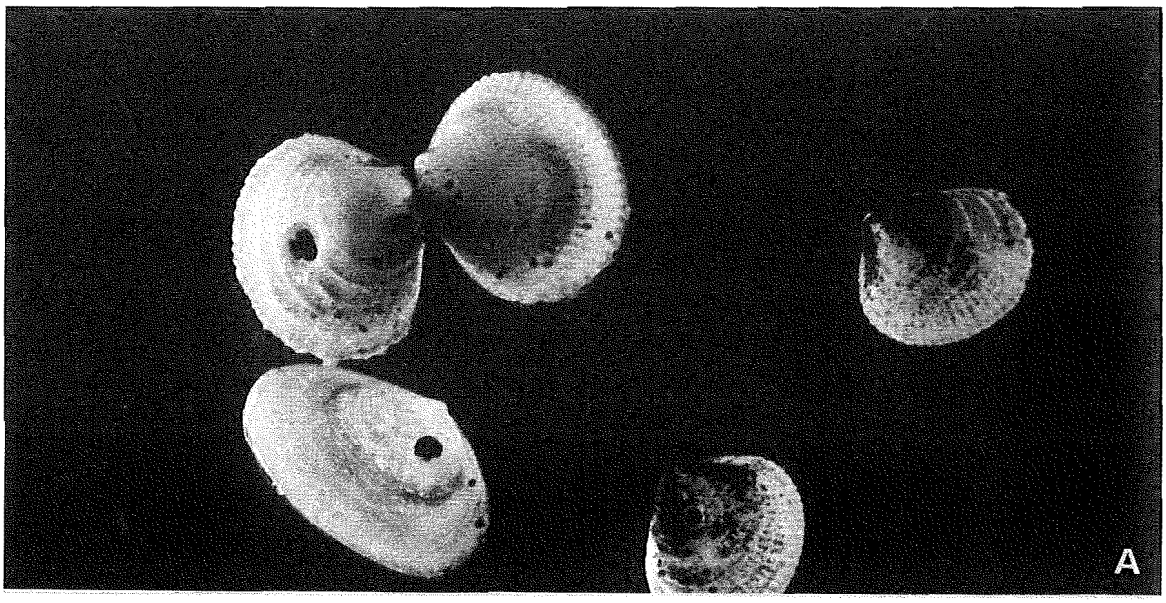
One significant and very well documented cause of mortality is predation by the South Island pied oystercatcher (*Haematopus ostralegus finschi*). Baker (1966, 1969, 1972, 1973) studied the oystercatcher

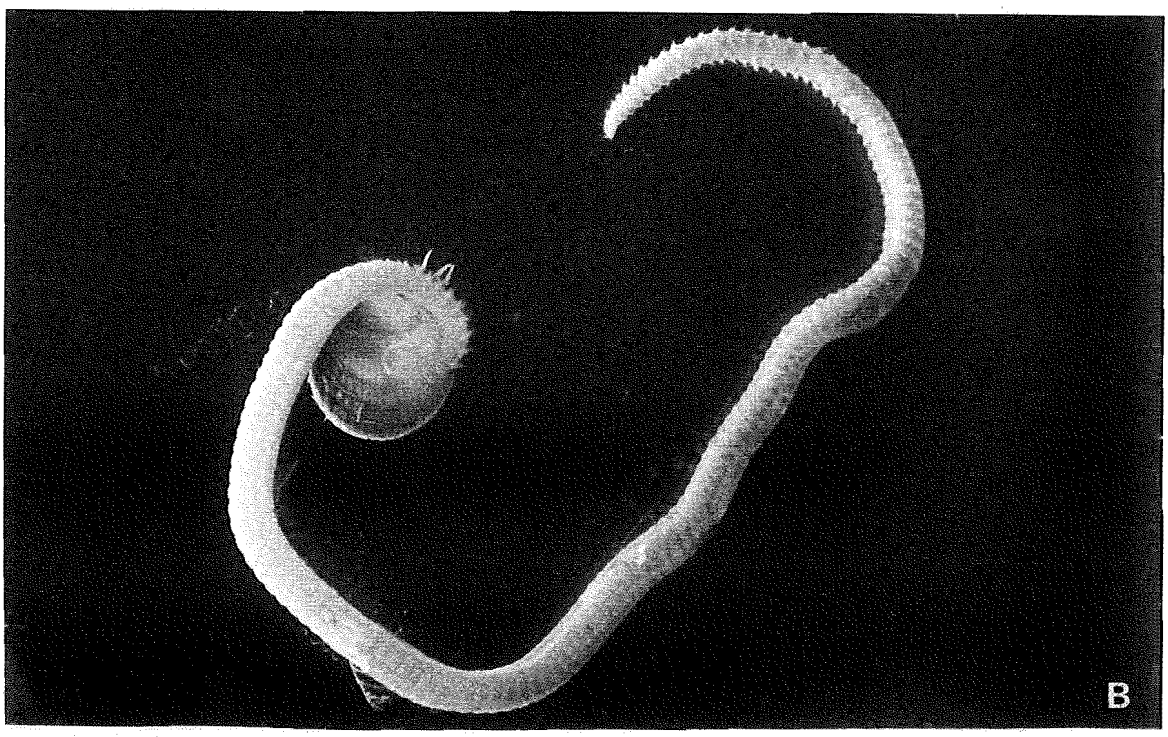
population of the Avon-Heathcote Estuary in detail, including feeding rates of the birds; and the relationship between the oystercatcher and the cockle is discussed further in section 5.2. Oystercatchers have been estimated to account for mortality equivalent to 4.17×10^{-2} and 8.3×10^{-3} g (dry organic matter) m^{-2} dy^{-1} in winter and summer respectively (Table 5.7). This is equivalent to 6.1×10^{7} g (dry *C. stutchburyi* tissue) yr^{-1} or 1.2×10^{9} kJ yr^{-1}. This estimate is based upon oystercatcher feeding rates and metabolic requirements, and not on actual records of *C. stutchburyi* mortality. Examination of a series of empty valves from the Avon-Heathcote Estuary reveals that mortality due to oystercatchers is concentrated in certain areas. One area of note is near the outfall from the Bromley oxidation ponds, where virtually all empty shells have a large hole in one valve characteristic of oystercatcher predation. There appears to be a positive relationship between the incidence of shell erosion by the worm *Polydora* sp. and mortality by oystercatchers, for the birds are able to prey upon very much larger shells than normal if they had been eroded. It is assumed that a size refuge is reached by *C. stutchburyi* in terms of oystercatcher predation because of shell thickness; and that this type of mortality is restricted to younger individuals (with thin shells) unless the shells have first been eroded by polychaetes. This is supported in part by evidence from the experimental plots (section 3.2) where large *C. stutchburyi* with thick shells lay loose and visible on the sediment surface for several months without any evidence of predation even though oystercatchers were feeding in the area.

The second significant cause of mortality is burial by shifting sediment. *C. stutchburyi* is relatively immobile (section 3.2) and is a relatively slow burrower. Inability to surface when buried by sediment has been noted (Stephenson, unpubl. data) and layers of dead buried *C. stutchburyi* in natural orientation are commonly taken in sediment cores from the Avon-Heathcote Estuary. In addition, the unimodal age class distribution of cockle populations is consistent with a sequence of major mortality in an area due to burial, followed by colonisation by a few year classes. Unfortunately, this aspect of mortality is very hard to quantify and is probably variable in its extent.

The third major type of mortality is in newly settled young-of-year. Mortality of juvenile *C. stutchburyi* was high, accounting for 40% of the estimated total settlement in the experimental plots in 1978 (section 3.2.4). These juvenile *C. stutchburyi* and also juvenile *Paphies australis* invariably had a small hole in one valve (Fig. 4.14 A).

Fig. 4.14 A (top); valves of juvenile *C. stutchburyi* (TL = 3.6, 2.7 mm) and *P. australis* (TL = 4.4 mm) showing holes attributed to *Aonides trifidus*. B (mid) and C (lower); juvenile *C. stutchburyi* (TL = 2.3 mm) with *Aonides trifidus* lodged in the hole in one valve.


A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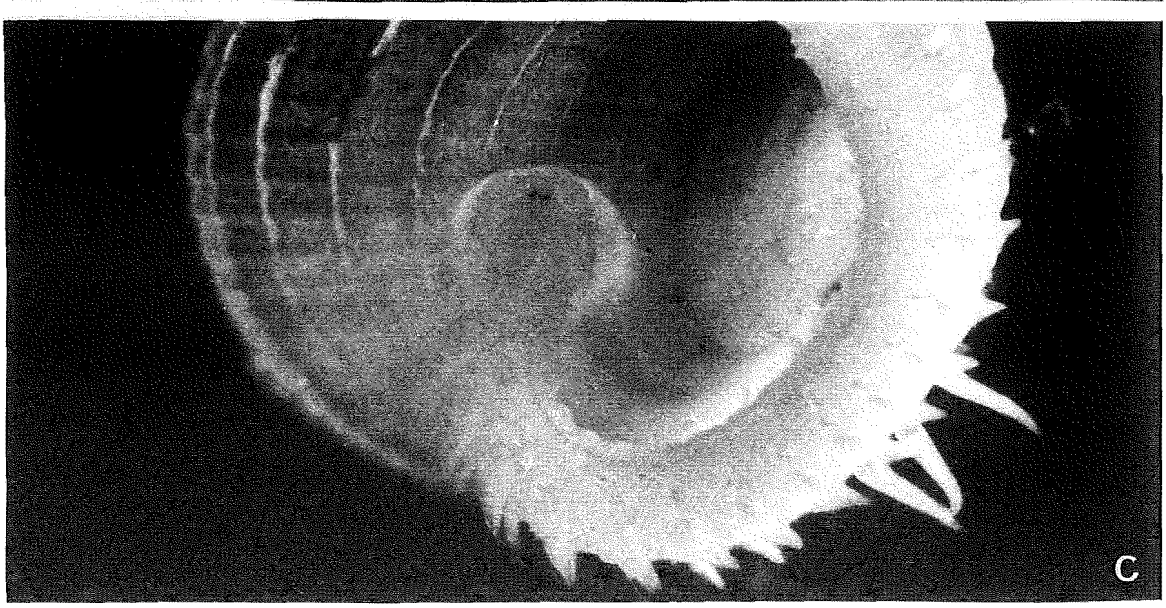
C

These holes are believed to have been bored by the polychaete *Aonides trifidus* since a juvenile *C. stutchburyi* shell was found with a worm still inside it (Fig. 4.14 B, C). *A. trifidus* was described from the Avon-Heathcote Estuary by Estcourt (1967) who recorded its occurrence at that time as "the most abundant polychaete (estimated maximum density 5000 per m^2) in the seaward part of the estuary. In sand and mud." While predation on the juvenile molluscs has not been observed, and no mechanism of shell boring by *A. trifidus* has been investigated, it is assumed to be responsible for the majority of the juvenile mortality in *C. stutchburyi*.

There are also several less important mortality agents. The whelk *Cominella glandiformis* preys upon *C. stutchburyi* especially those injured or dead, but its average density is low in the Avon-Heathcote Estuary and it is not considered to contribute significantly to total mortality. In the experimental plots (section 3.2) there was no evidence of significant predation by *Cominella glandiformis* even in cockles exposed on the sediment surface.

Webb (1973) studied the ecology of fish populations in the estuary and reported *C. stutchburyi* from the guts of flounder *(Rhombosolea plebeia* and *R. leporina)*, sole *(Peltorhamphus novaezeelandiae)* and yellow-eyed mullet *(Aldrichetta forsteri)*. Only in the yellow-bellied flounder *(R. leporina)* did molluscs account for more than 25% of the diet, and that was a mixture of *C. stutchburyi, Paphies australis* and *Amphibola crenata*. The significance of fish predation in the total mortality of *C. stutchburyi* is not known.

The shells of *C. stutchburyi* attract a range of epibionts, including the algae *Ulva lactuca* and *Gracilaria secundata*. Occasionally, these algae grow large enough for water currents to drag the alga with the cockle attached, out of the mud-flat and up onto the strand line. However, this accounts for a very small proportion of the total *C. stutchburyi* mortality.

An echinostome, *Curtuteria australis* that utilises *C. stutchburyi*, the whelk *Cominella glandiformis* and the oystercatcher *Haematopus ostralegus finschi* as hosts in its life history has been described from the Avon-Heathcote Estuary by Allison (1979). Cercaria are drawn into the mantle cavity of the cockle through the inhalent siphon and lodge in the foot muscle where metacercariae accumulate. A mean of 64% of

the cockles (and up to 79% of the older age classes) examined by Allison were infected and although an average of 3.3 metacercariae were recorded in large *C. stutchburyi*, little apparent physical damage is caused.

Human predation is potentially a very significant mortality factor, but is not so at present due to Health Department warnings not to eat shellfish from the Avon-Heathcote Estuary because of possible health hazards (Appendix IV).

4.8 FEEDING AND RELATED ASPECTS

4.8.1 Introduction

Ingestion and feeding are notoriously hard to document and quantify. While some of their qualitative aspects can usually be documented (for example food type through field observation, gut content analysis, etc.) quantitative data on feeding rates and food utilisation (digestion, assimilation) are less easy to obtain.

To make a realistic assessment of the role of an organism in a food chain, the natural food sources and the degree of utilisation of the foods must be known. In this study food utilisation by *C. stutchburyi* was investigated by stable carbon isotope analysis (section 4.8.2).

4.8.2 A stable carbon isotope study of *C. stutchburyi* and its food sources in the Avon-Heathcote Estuary

(Estuarine Research Report No. 22; 48 pp.)

A STABLE CARBON ISOTOPE STUDY OF *CHIONE (AUSTROVENUS) STUTCHBURYI* AND ITS FOOD SOURCES IN THE AVON-HEATHCOTE ESTUARY

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CONTENTS

1. INTRODUCTION

Although observations of what an animal ingests are relatively easily made (for example by field observation, gut content analysis, faecal analysis, etc.), these do not necessarily correspond to what the animal is assimilating and utilizing.

Methods of measuring what is assimilated, such as using radioactive isotopes as tags or comparative analysis of food, gut contents and faeces, are usually indirect and/or rely on a laboratory or other altered feeding situation.

In this study, the use of the stable isotopes of carbon as "natural tracers" is investigated in an attempt to define the food sources of *Chione (Austrovenus) stutchburyi* and other organisms of the Avon-Heathcote Estuary, Christchurch.

2. STABLE CARBON ISOTOPE RATIOS

Carbon is an appropriate measure of biomass and energy flow (Winberg 1971). It is the element that is initially reduced (gains electrons) during photosynthetic formation of organic carbon and which is subsequently oxidized during respiration, releasing the stored chemical energy to be used in plant and animal metabolic processes.

The organic carbon molecules produced by plants also provide the structural components of plant and animal tissues; i.e. biomass. Therefore, organic carbon is the "currency of exchange" of plant and animal communities (thus; standard measure of energy flow is gm $C \cdot m^{-2} \cdot day^{-1}$ etc.).

Recently the species of carbon has been considered. Carbon atoms possessing six neutrons and six protons (^{12}C) account for about 98.89% of the carbon atoms present on earth (= reference mass for atomic weight scale) while ^{13}C (seven neutrons and six protons) accounts for some 1.11% (Degens 1969, Hoefs 1980). These are the "stable isotopes" of carbon. The radioactive isotope, ^{14}C, accounts for one carbon atom in 10^{12}.

The precise ratio of the stable isotopes varies with the type of material analysed. The ratio $^{13}C : {}^{12}C$ is determined on CO_2 (see section 6.2.ii.) by mass spectrometry and is usually expressed with respect to a standard as:

$$\delta^{13}C_{PDB} \text{ per mil} = \left(\frac{^{13}C/^{12}C \text{ sample}}{^{13}C/^{12}C \text{ PDB standard}} - 1 \right) \times 1000$$

The PDB standard is the ratio of mass 45 to mass 44 in CO_2 prepared from the fossil skeleton of a Cretaceous belemnite (extinct cuttlefish) *Belemnitella americana*, from the Pee Dee formation of South Carolina (Craig 1957). $\delta^{13}C$ is the difference per mil (‰) of the $^{13}C/^{12}C$ ratio of the sample and that of the PDB standard.

The naturally occurring variation of $\delta^{13}C$ is greater than 100‰(excluding meteoritic carbonate) with heavy carbonates possessing δ-values of more than +20, and light methane of about -90‰ reported in the literature (Hoefs 1980, Schwarcz 1969).

The $^{13}C/^{12}C$ ratio of atmospheric CO_2 is smaller than that of the PDB standard by 0.7% (7 per mil) and the $\delta^{13}C_{PDB}$ is therefore -7‰.

Carbon is present in two main reservoirs; organic matter and sedimentary carbonates, which are isotopically distinct because of the operation of two different reaction mechanisms (Hoefs 1980):

1) a kinetic effect during photosynthesis leading to concentration of the light ^{12}C in synthesized organic material (and depletion of ^{12}C in the remaining CO_2);

2) a chemical exchange effect in the atmospheric CO_2 - dissolved HCO_3^- system, which leads to an enrichment of ^{13}C in the bicarbonate (Deuser and Degens 1967).

3. DEVELOPMENT OF $\delta^{13}C$ APPLICATION

A.O. Nier and co-workers first measured variations in the $^{13}C/^{12}C$ ratios of plants and animals, and showed that the isotopic composition of carbon in living matter and related materials is different from that in carbonates (Nier and Gulbransen 1939, Murphy and Nier 1941). Organic matter is enriched in the lighter ^{12}C (depleted in ^{13}C).

Work continued mainly on inorganic carbon isotope ratios and their use in geology (Rankama 1948; Wickman et al. 1951, Wickman and von Ubisch 1951) until Wickman (1952) (pointing out how little work had been done on "recent" material) surveyed the stable carbon isotope ratios of 105 herbarium plants representing all the major taxonomic groups. He concluded that the ^{13}C depletion in plants is intimately connected with the cycle of atmospheric CO_2; that in places where the cycle cannot develop (e.g. open sea or desert) depletion is much less than where the cycle is much more complete and intense (e.g. tropical rainforest or stagnant water). No principal systematic differences were noted between groups (except perhaps the gymnosperms) but characteristic differences were apparent between plants growing in different biotypes.

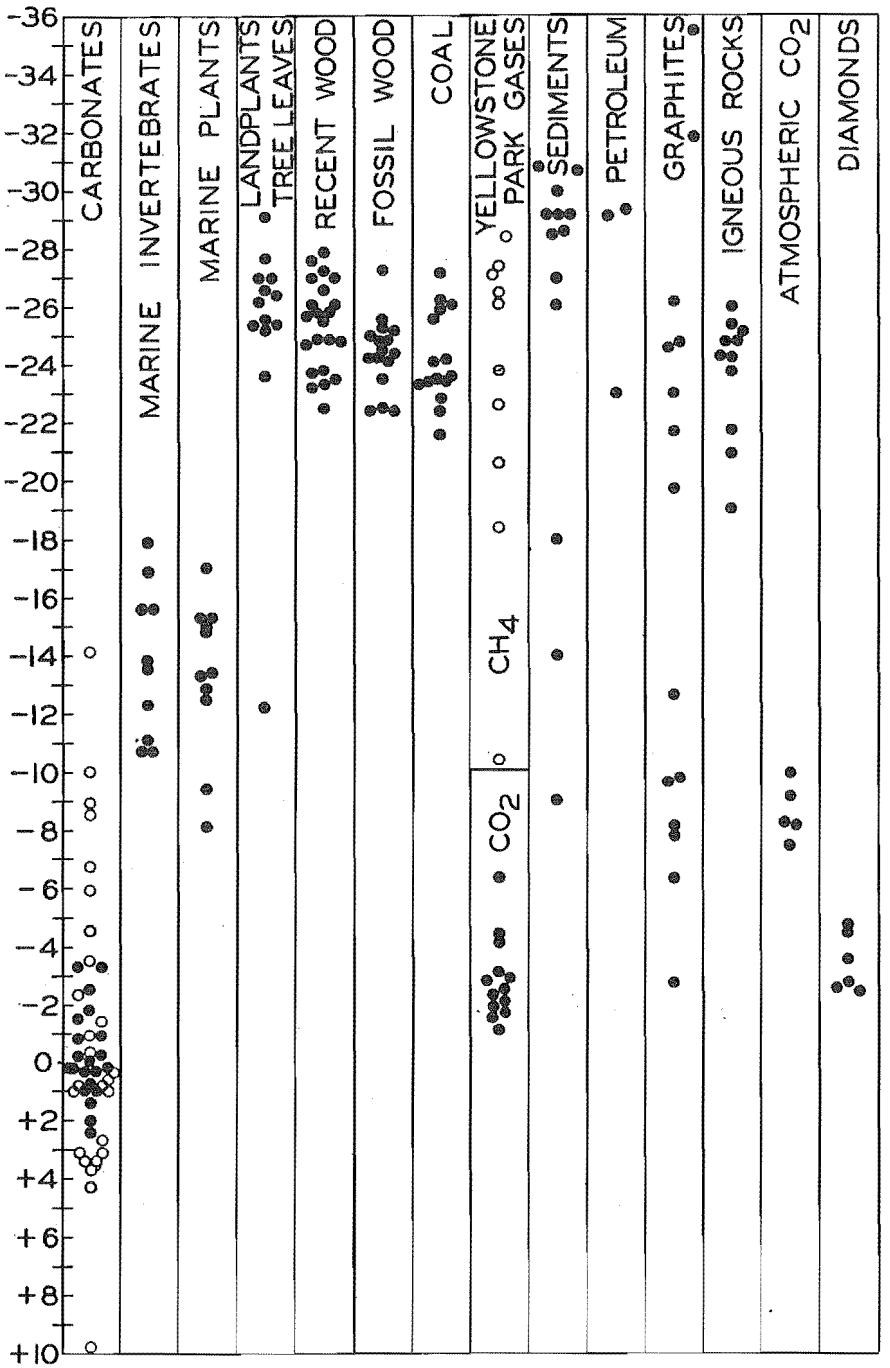
Craig (1953) undertook an extensive survey of the variation of the $^{13}C/^{12}C$ ratio in nature analysing several hundred samples from various geologic sources, and a few organic sources. Terrestrial organic carbon and carbonate rocks constituted well defined groups; the carbonates being richer in ^{13}C by some 2% (20‰). Marine organic carbon was reported to lie in a range "intermediate between the groups" (Fig. 3.1).

In the 1950's and early 1960's petroleum geologists made use of the relative difference in ^{13}C depletion of terrestrial and marine plants pointed out by Wickman (1952) and Craig (1953) in attempting to explain the derivation of sediment organic carbon and petroleum deposits (Craig 1953, Landergren 1954, Silverman and Epstein 1958, Eckelmann et al. 1962, Sackett and Thompson 1963, Sackett 1964, Parker et al. 1972). Some of these included estimates of the relative contribution of marine and terrestrial or freshwater plants to sediment and petroleum deposits.

A logical, and very significant progression of the work on nearshore marine sediments was that of Parker (1964) in which the stable carbon isotope ratios of the members of a marine community (Redfish Bay, Texas) were measured to determine the magnitude of the isotope ratio variations that might occur in a semiclosed system for which the ultimate source of all carbon is the bicarbonate of sea water. The study included investigation of the ratio differences in total, lipid, and protein-carbohydrate carbon of representatives of several trophic levels. Two very significant observations were made:

1) that there was a range of $\delta^{13}C$ values from -6 to -17‰ among members of the community,

2) the ratio was constant (± 1‰) for different individuals of the same species;



δ C^{13}/C^{12} in $^{0}/_{00}$, of various carbonaceous samples.

Fig. 3.1 $\delta^{13}C$ values of various carbonaceous samples presented by Craig 1953: 60.

and also that:

3) pure fatty acids and/or lipids were 0.5 to 15‰"lighter" than the whole organism total carbon,

4) the organic matter of the sediment could have been supplied by the community according to the carbon isotope data.

Thus the scene was set for the use of stable carbon isotopes in community food web studies - however this took a few years to take place.

4. PHOTOSYNTHETIC FRACTIONATION OF STABLE CARBON ISOTOPES

It is a feature of all plants that the ratio of naturally occurring stable carbon isotopes is different from the ratio in air (Fig. 4.1).

In addition to the marine/terrestrial difference in ratio, Wickman (1952) reported that some terrestrial plants were relatively rich in ^{13}C. This was overlooked for several years (Smith 1972) even though occasional results confirmed it (Craig 1953, Broecker and Olson 1959, Emery et al. 1967, Oana and Deevey 1960). Bender (1968) was the first to realize that isotopic differences between some tropical and temperate grasses represented heritable metabolic adaptations to certain environments (Smith 1972).

Terrestrial higher plants contain less ^{13}C relative to ^{12}C than is present in the CO_2 of air (Troughton and Card 1975) and are now known to differ in $\delta^{13}C$ values according to the metabolic pathway used during photosynthetic fixation of CO_2 (Park and Epstein 1960, Troughton et al. 1974A, Cristeller et al. 1976, and others).

A clear distinction has been shown between plants utilizing the C_3 or Calvin pathway and those using the C_4 or Hatch-Slack pathway (Hatch and Slack 1970) of double carboxylation (Bender 1971, Smith and Epstein 1971, Smith et al. 1976) and more recently, those utilizing the CAM (Crassulacean Acid Metabolism)-diurnal process of acidification and deacidification (Bender et al. 1973, Osmond et al. 1973).

Fractionation occurs at the initial carboxylation sites of ribulose-1,5-biphosphate (RuBP) carboxylase in C_3 plants (Park and Epstein 1960) and phosphoenolpyruvate (PEP) carboxylase in C_4 plants (Whelan et al. 1970, Whelan et al. 1973). Fractionation apparently results from differences in discrimination towards ^{13}C by the carboxylase enzymes (Benedict 1978, Smith 1972, cited in Guy et al. 1980). The $\delta^{13}C$ values resulting from fractionation by these paths are as follows (Bender 1971, Smith and Epstein 1971, Troughton 1971, Bender et al. 1973, Hoefs 1980):

photosynthetic pathway	$\delta^{13}C$ (‰) range	mean
C_3	-23 to -37	-27
C_4	-9 to -16	-12
CAM	-11 to -33	-17

(See also Osmond et al. 1975, Troughton and Card 1975).

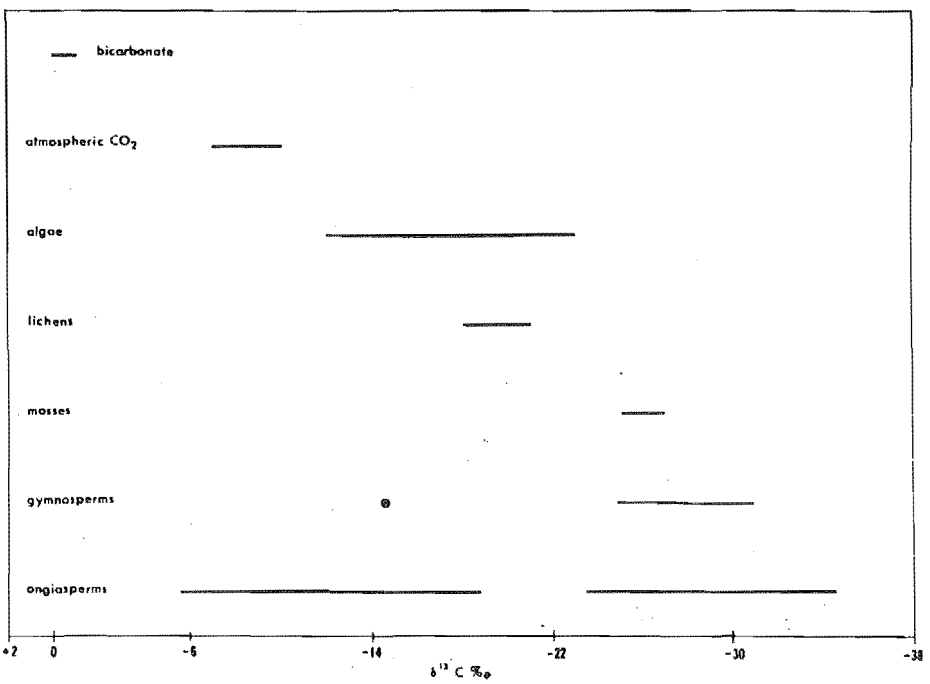


Fig. 4.1 $\delta^{13}C$ values for plants.
From Smith (1972):227.

While the total carbon $\delta^{13}C$ of C_3 and C_4 species does not usually vary by more than one or two per mil, even from widely separated geographic locations (Smith and Brown 1973), CAM species are often subject to broad, environmentally induced (spatial) fluctuations (Bender et al. 1973) presumably reflecting relative contributions of carbon fixed by RuBP and/or PEP carboxylases (Bender et al. 1973, Lerman et al. 1974, Osmond et al. 1973, cited in Guy et al. 1980).

Small isotopic differences exist among plant organs and biochemical fractions (Emery et al. 1967, Lowdon 1969, Parker 1964, Smith and Epstein 1970). Troughton and Card (1972) noted a slight detectable variation between parts of a plant (<2.3‰ in potato) and slightly more among growth stages of wheat (4‰). Although Jansen (1962), and Craig (1954) have noted variation in the $\delta^{13}C$ values of wood from very old kauri and Sequoia trees these changes are possibly due to changes in proportional composition of the tree tissue (Stout et al. 1975). These trends of $\delta^{13}C$ in young wood may also be attributed to the young trees being in dense forest and some of their air CO_2 being respired from other trees and hence lighter, than adult trees reaching above the canopy into well mixed atmosphere.

5. $\delta^{13}C$ IN FOOD WEB STUDIES - A REVIEW

Once fixed in plant material during photosynthesis the $\delta^{13}C$ is not changed even by death and subsequent decay (Smith and Epstein 1970). Detritus (formed under aerobic conditions) has the same $\delta^{13}C$ as the plant from which it is derived (Haines 1977).

Further, animals assume very nearly the $\delta^{13}C$ of the diet.

Smith and Epstein (1970) investigated the $\delta^{13}C$ values of 14 plant species from a salt marsh and lagoon. They observed 1) that plants discriminate against ^{13}C, particularly in the lipid fraction, and 2) that herbivore tissues reflected the isotope ratios of plants ingested.

Minson, Ludlow and Troughton (1975) made the first comparison of the $\delta^{13}C$ of higher animal tissue with that of its food. Hair and milk of cattle (representing the products of long and short term absorption of nutrients respectively) were compared with pastures composed of temperate C_3 or tropical C_4 grasses on which the animals had been raised. The carbon ratios of the animals reflected those of the food source as follows:

$^{13}C/^{12}C$ ratios of pasture and of milk and hair of grazing cattle

Pasture location		Pasture species	Photosynthetic pathway	No. of cows	Time since calving (d)	$\delta^{13}C$ parts per ml Pasture	Milk	Hair
Swan's Lagoon, Qld	20°10'S, 147°15'E	*Heteropogon contortus*	C_4	3	45	−14.0	−15.5	−12.1
Wollongbar, NSW	28°50'S, 153°25'E	*Pennisetum clandestinum*	C_4	3	107	−12.4	−13.0	−15.1
Murray Bridge, SA	35°07'S, 139°16'E	**Lolium perenne*	C_3	1	120	−25.4	−22.5	−22.3
Werribee, Vic.	37°54'S, 144°39'E	**Lolium perenne*	C_3	1	210	−28.9	−26.0	−26.2

*Also *Trifolium repens* and other temperate species.

(from Minson et al. 1975; p602)

with a minor variation probably caused by ^{13}C discrimination by rumen organisms or within the tissues of the animal and/or by selective grazing of certain plants.

Burleigh and Brothwell (1978) found that the $^{13}C/^{12}C$ ratio of the hair of dogs is affected by the presence of maize in the diet.

Lyon and Baxter (1978) measured the $^{13}C/^{12}C$ ratio in over 80 samples of human tissue and showed that the natural isotope ratios were unaffected by tissue type, age or sex and were similar for cancerous and healthy human tissue.

Webb et al. (1980) noted a difference greater than 4‰ between $\delta^{13}C$ values of hair of residents of Brisbane, Australia (subtropical) and Wellington, New Zealand (temperate) as follows:

Country	Dietary habits	No. of people	$\delta^{13}C$ parts per ml	
			Mean	Standard deviation
Queensland	Ovo-lacto vegetarians	5	−18.46	± 1.08
	Meat eaters	5	−18.46	± 0.58
	Mean	10	−18.46	± 0.82
New Zealand	Ovo-lacto vegetarians	22	−23.10	± 1.06
	Meat eaters	12	−22.48	± 1.22
	Mean	34	−22.88	± 1.14

$\delta^{13}C$ content of hair samples of residents of Queensland and New Zealand

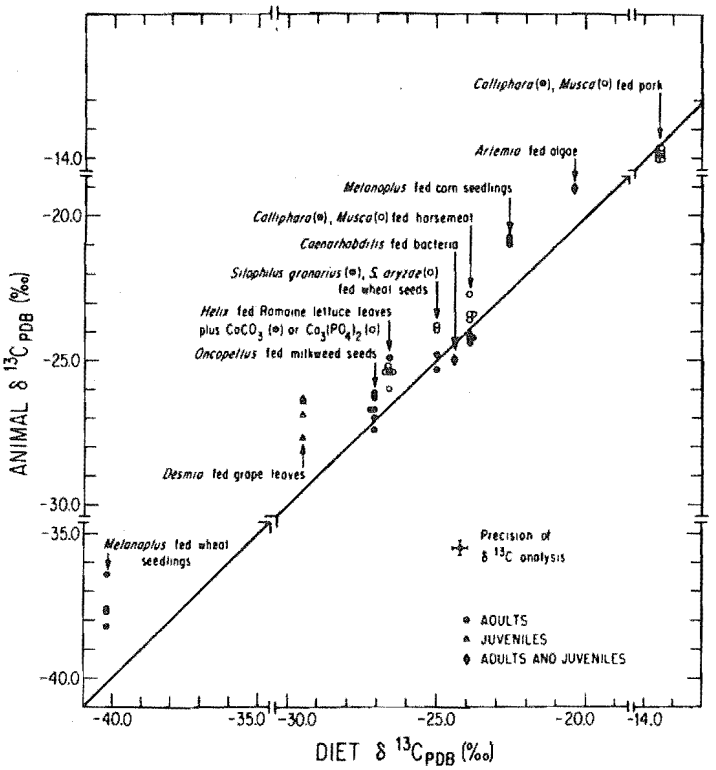
(from Webb et al. 1980; p 201)

and related this to differences in the plant groups supporting meat production in the two areas. No significant difference was noted in the ratios of ovo-lacto vegetarians and meat eaters in each country.

DeNiro and Epstein (1978) investigated the distribution of carbon isotopes in animals grown in the laboratory on diets of constant carbon isotopic composition. Whole body isotopic composition reflects that of diet, but the animal is enriched in ^{13}C by 1‰ relative to diet (Fig. 5.1). Also, $\delta^{13}C$ of whole bodies of individuals of the same species raised on the same diet may differ up to 2‰. In three of four cases, ^{13}C enrichment of the whole body is balanced by ^{13}C depletion of respired CO_2.

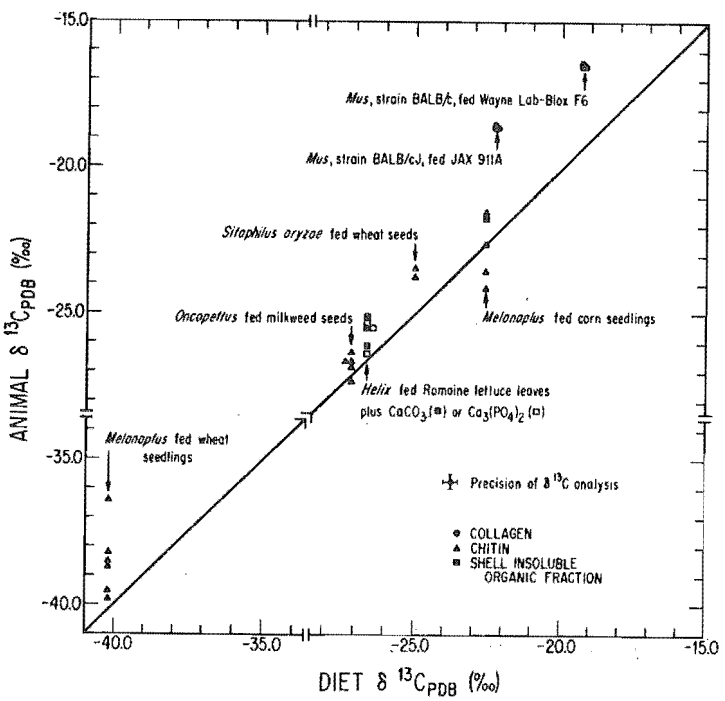
Many of the isotopic relationships among the major biochemical fractions (lipid, carbohydrate and protein) are qualitatively preserved as diet carbon is incorporated into the animal. However, the difference in $\delta^{13}C$ of a biochemical fraction in the animal and in its diet may be as much as 3‰. The $\delta^{13}C$ values of the biochemical components collagen, chitin and the insoluble organic fraction of shells, all of which are often preserved in fossil material, are related to the isotopic composition of the diet (Fig. 5.2).

They state that while the limits of accuracy of this method will generally restrict its application to situations in which the diet is derived from sources with relatively large differences in $\delta^{13}C$ values (such as terrestrial vs aquatic organisms or C_3 vs C_4 plants), the method should be applicable to fossil as well as living material.



$\delta^{13}C$ values of the whole bodies of animals and their diets. Each point represents the analysis of a single animal, except for the two *Sitophilus* species (five animals were combusted together for each point) and for *Artemia* and *Caenorhabditis* (many animals were combusted together for each point).

Fig. 5.1 Relationship between $\delta^{13}C$ values of animal tissues and that of their diets. From DeNiro and Epstein 1978: 499.



$\delta^{13}C$ values of some biochemical components of animals which are often preserved in fossil material and their diets. Each point represents the analysis of the specified component isolated from a single animal, except for *Sitophilus oryzae* (chitin samples from ten animals were combusted together for each point).

Fig. 5.2 $\delta^{13}C$ values of some biochemical components of animals which are often preserved in fossil material, and their diets. From DeNiro and Epstein 1978: 504.

Teeri and Schoeller (1979) in a simple but informative experiment reared *Tribolium* beetles in mixtures of flour ranging from 100% C_3 to 100% C_4 plant material. Whole body isotope ratios were closely correlated with the $\delta^{13}C$ of the diet, and the degree of correlation was independent of the growth rate of the animals.

The relationship of plant and animal stable carbon ratios in a food chain may be represented as in Fig. 5.3. Plant carbon is depleted in ^{13}C (with respect to the atmosphere) according to its physiology. Subsequent "processing" of carbon in a food chain results in ^{13}C enrichment at each step of the food chain.

This has allowed the use of $\delta^{13}C$ as natural tracers of plant carbon in several habitat types. A few studies are reviewed here to illustrate the lines and diversity of application of this technique.

Land et al. (1975) and Black and Bender (1976) have related the carbon isotope composition of coral tissue, to that of its endosymbiotic zooxanthellae.

Haines (1976A) studied six intertidal zones of a salt marsh near Sapelo Island, Georgia, on a 300 m transect. Salt marsh plants segregated isotopically into three groups:

group	$\delta^{13}C$ (‰)
grasses (including *Spartina alterniflora*)	-12.3 to -13.6
other vascular plants	-22.8 to -26.0
benthic diatoms	-16.2 to -17.9

Marsh soils and to some extent the invertebrate fauna reflect the carbon isotope composition of the major primary producer species in the various zones. Five samples of particulate organic carbon in marsh tidal water (0.5 - 1ℓ filtered on to glass fibre papers) were -19.8 to -22.8‰. These are within the values found for offshore P.O.C., most of which is presumed to originate from phytoplankton photosynthesis; casting doubt on assumptions that the bulk of detrital carbon in Georgia estuaries is derived from *S. alterniflora* production (see also Haines 1977 in which estuarine seston $\delta^{13}C$ is compared with that of marine phytoplankton, terrestrial detritus and *Spartina* detritus, with the same conclusion).

In contrast to this, Peterson et al. (1980) point out (in a theoretical paper) that the $\delta^{13}C$ value of *Spartina* litter could be depleted in ^{13}C during colonization and decomposition by bacteria under anaerobic conditions (Fig. 5.4).

Haines (1976B) found that carbon isotope ratios of the detritivore *Uca pugnax* (fiddler crab) feeding in mono specific and mixed stands of C_3 and C_4 salt marsh plants were linearly related to the $^{13}C/^{12}C$ ratios of the plants. The relation between crab and marsh soil ratios was less direct. The isotopic composition of the crab carbon was observed to be biased toward the ratio of C_4 plants and it is suggested that this may be due to the relative palatability of, or preference for, these plants.

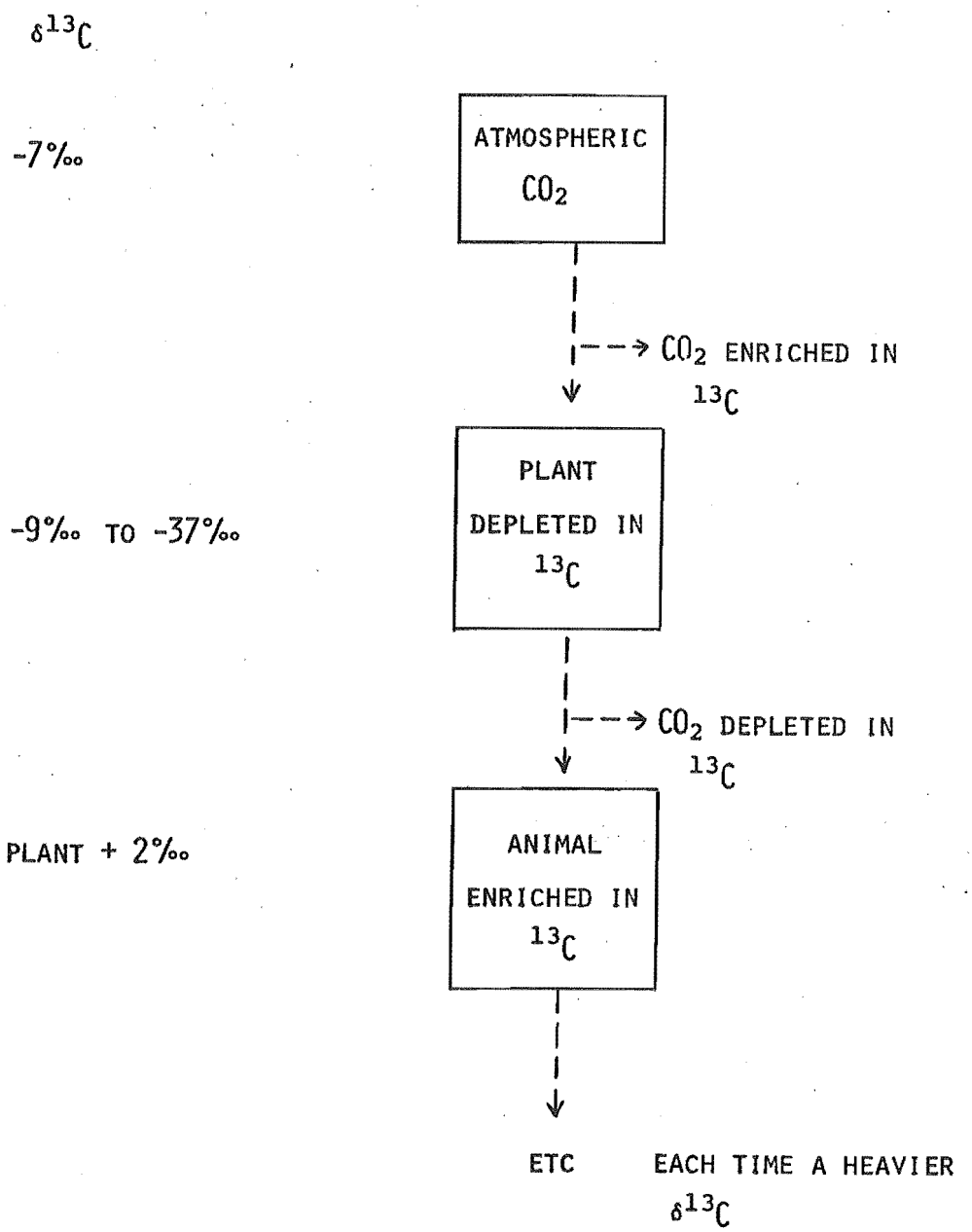
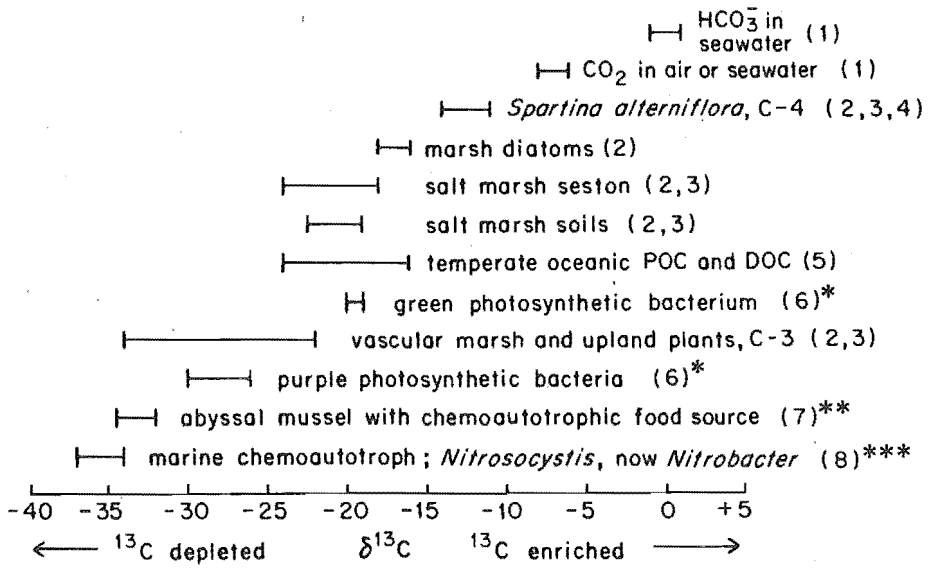


Fig. 5.3 The relationship of plant and animal stable carbon isotope ratios in a food chain



Carbon isotope ratios for selected components of marine ecosystems, with emphasis on salt marshes. Results are expressed as parts per thousand deviation from the PDB carbonate standard.

$$\delta\ ^{13}C = \frac{^{13}C/^{12}C \text{ sample}}{^{13}C/^{12}C \text{ standard}} - 1 \times 1000$$

Numbers in parentheses are references: (1) Deuser and Degens 1967, (2) Haines 1976, (3) Haines 1977, (4) Valiela et al. 1978a, (5) Degens 1969, (6) Sirevag et al. 1977, (7) Rau and Hedges 1979, (8) Degens et al. 1968.

* We calculated these carbon isotope ratios from the fractionation observed in laboratory culture but assuming the source CO_2 has a $\delta\ ^{13}C$ of –7‰. The green photosynthetic is *Chlorobium thiosulfatophilum* and the purples are *Rhodospirillum rubrum* and *Chromatium* spp.

** Since consumers do not appear to fractionate the carbon in their food to any major extent, we expect that the chemoautotrophic sulfur bacteria which the mussel probably uses for food is similar in isotopic composition but the actual diet of the mussel is unknown and the isotopic composition of the food has also not been measured.

*** This is not a sulfur utilizing bacterium but we expect sulfur using chemoautotrophs might be similar. The carbon isotope ratio is calculated from the fractionation in laboratory culture assuming the natural source CO_2 has a $\delta\ ^{13}C$ of –7‰.

Fig. 5.4 Relationship between $\delta^{13}C$ values of components of the salt marsh ecosystem, and bacteria presented by Peterson et al. 1980: 175.

Fry, Joern and Parker (1978) report; 1) that 25 species of grasshopper have stable carbon isotope ratios similar to that of the diet; 2) that males and females of the same species reflect similar diets and ratios, and 3) that specialist individuals (of the same species feeding on the same diet) show a range of $\delta^{13}C$ of 1.6‰ or less, but that generalist species which feed upon substantial amounts of both C_3 and C_4 plants show larger individual variation. They conclude that the average $\delta^{13}C$ of a species, and the variability among individuals are both useful in predicting grasshopper diet in terms of mixtures of C_3 and C_4 plants.

Fry and Parker (1979) analysed $\delta^{13}C$ of over 340 animals from Texas estuarine seagrass meadows and nearshore Gulf of Mexico. Fish and shrimp collected in seagrass beds were significantly enriched in ^{13}C (by an average of 3.3 to 5.1‰) relative to comparable animals (different species) collected offshore. This is attributed to the contribution of salt marsh vegetation to the diet, since animals of the salt marsh ($\delta^{13}C$ about -12‰) are heavier in ratio than those of open water (-19‰) or even an estuarine bay lacking sea grasses (-19‰). One polychaete worm (*Diopatra*) of the seagrass meadow was 8.3‰ enriched relative to specimens collected in areas where phytoplankton were major primary producers. The authors use their data to support the notion that sea grasses and other benthic plants are significant sources of nutrition for juvenile shrimp and fish in Texas bays. (Note: the same authors presented a paper at the 43rd Annual Meeting of the Amer. Soc. of Limnol. and Oceanography, Univ. of Tennessee, June 16-19 1980; entitled "migratory shrimp in the northern Gulf of Mexico - $\delta^{13}C$ evidence for estuarine dependence".)

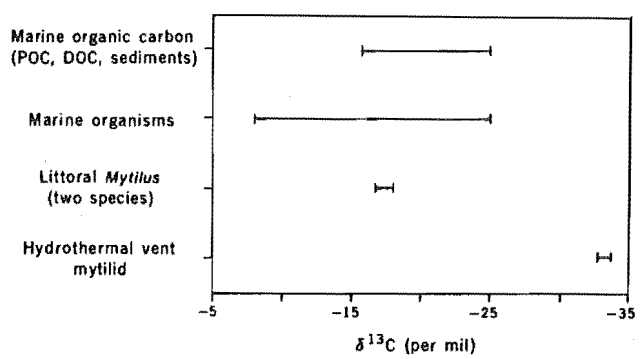
McConnaughy and McRoy (1979A,B) have investigated isotopic fractionation within the food web of the Bering Sea and have been able to identify the Eelgrass (*Zostera marina*) contribution.

Tieszen et al. 1979 measured $\delta^{13}C$ of food in the rumen of East African herbivores and found that the results were within 1% of estimates based on direct quantitative visual analysis of gut contents. The isotopic method of determining C_3 and C_4 plant contribution to the diet was just as accurate, and had the advantage of being more rapid and totally objective.

Differentiation was possible between grazers (Konyoni, wildebeest, cattle and sheep); browsers (Grant's gazelle); and those intermediate (Thompson's gazelle, goats and impala). In addition, a marked and rapid shift from browsing to grass was documented after a rain (Tieszen *et al.* 1979).

Rau and Hedges (1979) noted that tissues of a mytilid mussel from a hydrothermal vent (2500 m depth) in the Galapágos Rift zone are strikingly depleted in ^{13}C relative to the tissues of other marine organisms and normal marine food sources (Fig. 5.5). They interpret this as indicating the utilization of a chemosynthetic bacterial food source.

Rau (1980) identified three primary organic sources of carbon for a small sub-alpine lake in Washington; conifer tree detritus (mean $\delta^{13}C$ = -27.3‰), periphyton (-34.6‰) and plankton (-45.9‰).



The $\delta^{13}C$ of organisms and major organic carbon reservoirs in temperate ocean environments including pelagic and bathypelagic animals (*3*, *4*), particulate organic carbon (*POC*), dissolved organic carbon (*DOC*), and sediments (*4*, *5*). Also shown is the range of seven $\delta^{13}C$ determinations of foot and mantle tissues from two littoral *Mytilus* species and the range of eight determinations on the same types of tissue from a hydrothermal vent mytilid.

Fig. 5.5 Relationship of the $\delta^{13}C$ value of a hydrothermal vent mussel to that of other mussels and marine organisms. From Rau and Hedges 1979: 648.

He noted that these ratios were reflected in aquatic insects of various feeding modes, and was able to estimate the portion of insect carbon leaving the lake during adult insect emergence which was of terrestrial origin.

In a series of publications, Tan and co-workers (Tan and Walton 1978, Strain and Tan 1979, Tan and Strain 1979A,B) have investigated the inorganic and organic stable carbon isotope ratios of particulate matter, water and sediments of the Gulf of St Lawrence in an attempt to identify sediment sources, sedimentation rates including the seaward extent of terrestrial organic matter influence, and water currents.

In a similar line, Kroopnick et al. (1972) have estimated the relative contribution of organic, and carbonate derived carbon to deep sea CO_2; Deuser (1970) has elucidated the carbon sources responsible for H_2S concentrations in an anoxic basin; and several workers have investigated the mixing and characterisation of water masses (Sackett and Moore 1966; Mook 1970, 1971).

6. A STABLE CARBON ISOTOPE STUDY OF THE AVON-HEATHCOTE ESTUARY

6.1 Introduction

As part of a study aimed at defining the role of an invertebrate species (the New Zealand cockle, *Chione (Austrovenus) stutchburyi*) in the energy flow of the Avon-Heathcote Estuary, Christchurch (Stephenson in prep.), a stable carbon isotope study of *Chione*, other members of the benthic macrofaunal community and some of their food sources was undertaken.

The Avon-Heathcote Estuary (AHE) is a small (6 km^2 area), shallow (mean depth at HWOST = 1.4 m) bar built estuary. It is largely intertidal (85% of area is intertidal mudflat) with almost complete tidal exchange. It has a drainage basin of approximately 200 km^2, over half of which is the urban area of the City of Christchurch (population approximately 300,000) (Fig. 6.1; see also Knox and Kilner 1973, McPherson 1978).

Chione is a sediment-dwelling filter feeder common to many New Zealand estuaries and protected bays (Morton and Miller 1973). It is present in most of the AHE, reaching densities greater than 3000 m^{-2}, a maximum recorded biomass of 465 g AFDW$\cdot m^{-2}$ and a maximum calculated production of 20 g AFDW$\cdot m^{-2} \cdot yr^{-1}$ (Stephenson unpubl. data).

Although *Chione* is known to be a filter feeder (Morton and Miller 1973, Larcombe 1971), its food sources and the degree of utilization of these foods have not been investigated.

Chione has short siphons, is relatively immobile and lives in an environment prone to high suspended particle load due to wind mixing. It is not surprising then, that preliminary analysis of gut contents (Stephenson, unpub. data) reveals a wide range of particle types, including a great deal of higher plant detritus and sediment. The range of particle types corresponds well with that of overlying water indicating that *Chione* is an indiscriminate filter feeder.

It is of great interest then, in terms of both the biology of the animal, and its role in the estuarine system, to determine:

1) what food source is being actually assimilated and used; and

2) what is the origin of the food source?

The AHE receives freshwater input from the Avon and Heathcote Rivers and from the Bromley oxidation ponds, as well as seawater input. The magnitude of these flows are represented in Fig. 6.2.

There is an area of ponding just outside the estuary that is not truly marine, and 44% of the outflowing water returns on the next tide (Knox and Kilner 1973). McCormacks Bay, which has been isolated by a causeway from the rest of the estuary has an altered tidal regime and elevated salinity.

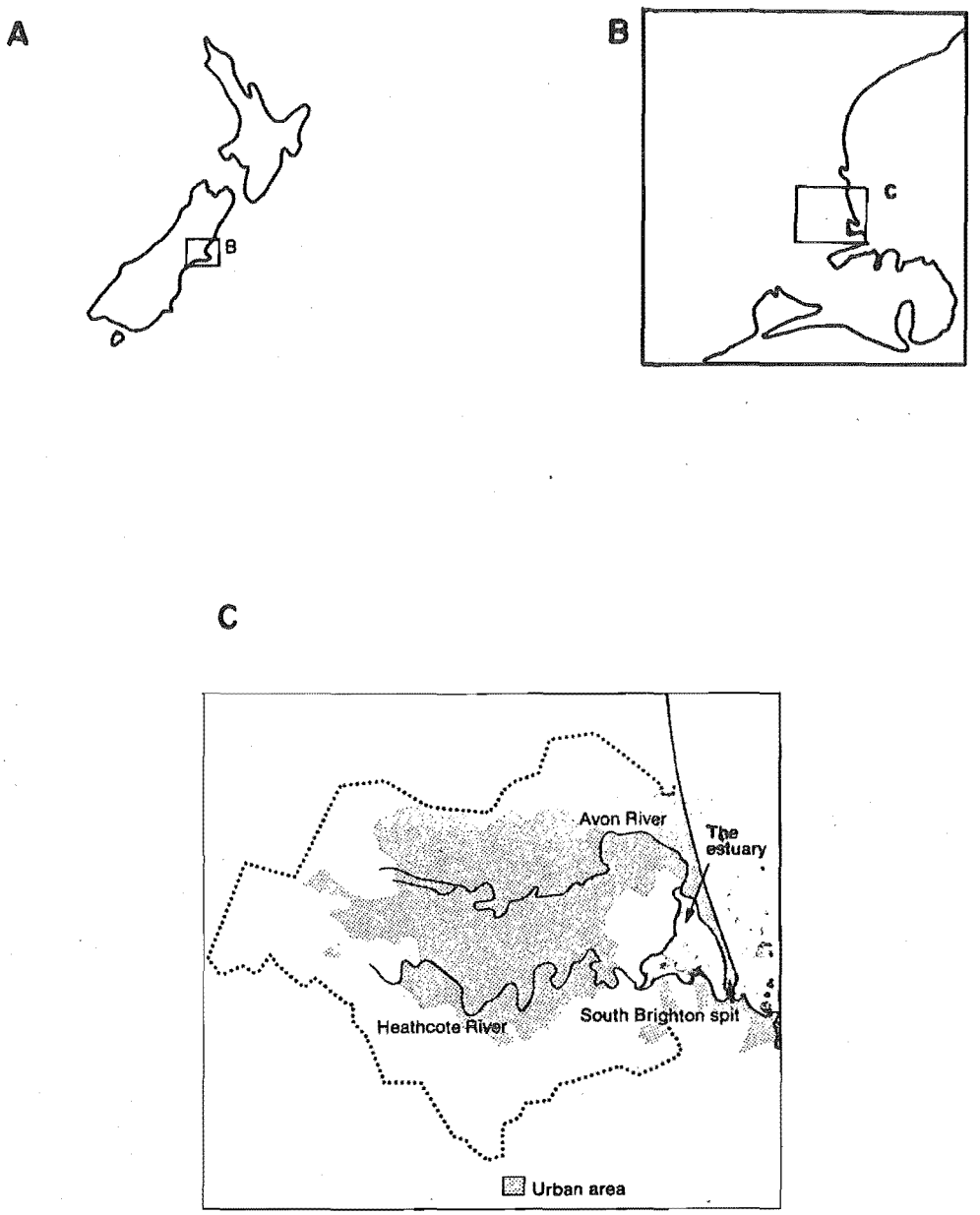
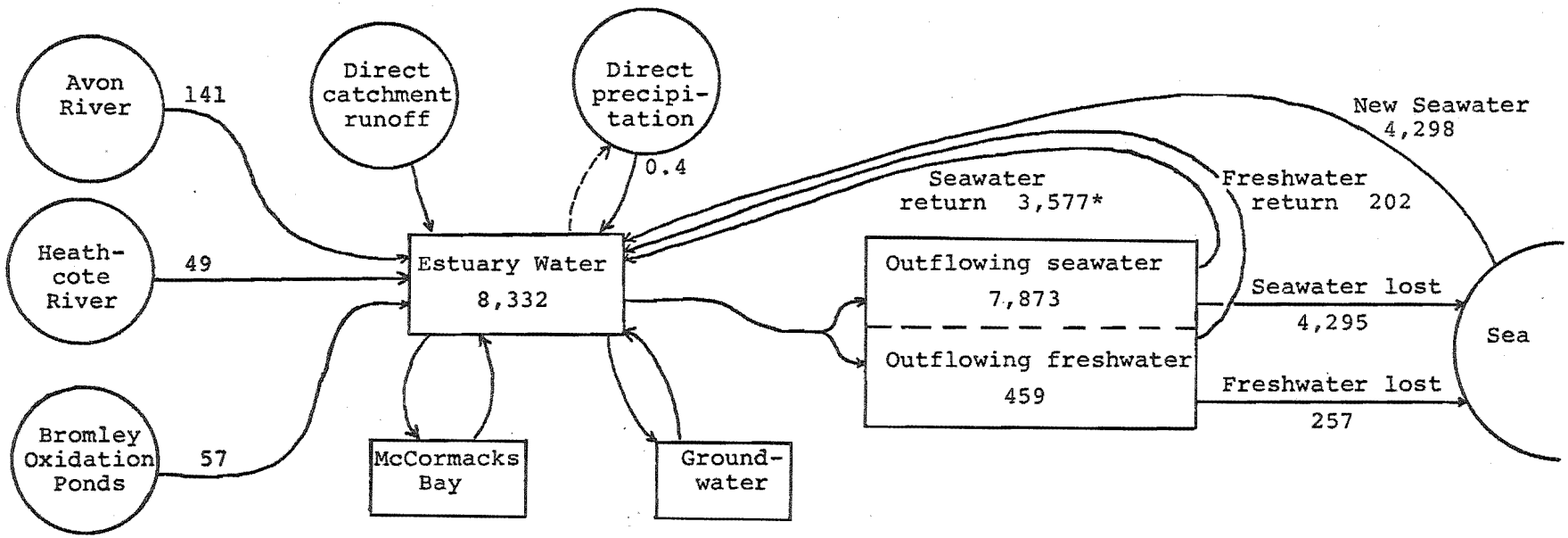


Fig. 6.1 Location of the Avon-Heathcote Estuary, Christchurch, New Zealand



Avon-Heathcote Estuary, Hydrology, Mean tide volumes (m^3 x 1000)

* based upon 44% return of freshwater

Fig. 6.2 Hydrology of the Avon-Heathcote Estuary

The proportional nutrient supply to the AHE by the freshwater sources is depicted in Fig. 6.3. Note the degree to which the oxidation pond discharge dominates the nutrient flow in the estuary.

There should be only five possible food sources for *Chione* in this system:

1) Marine phytoplankton carried into the estuary on the incoming tide.
2) "Freshwater" phytoplankton from the two rivers and oxidation ponds.
3) Detritus fragments derived from terrestrial vegetation.
4) Benthic microflora and diatoms, and detritus of benthic algae (such as *Ulva*).
5) Bacteria, colonizing detritus and sand particles.

This would seem an ideal situation for a stable carbon isotope study of the food web, since there are only a few carbon sources and a great possibility that they would be isotopically distinct as follows:

1) organic matter derived from oceanic HCO_3^- (such as marine phytoplankton and estuarine algae) is distinct from that derived from atmospheric CO_2 (terrestrial plants) (Hoefs 1980, and others);
2) the terrestrial flora of New Zealand is composed of plants which tend to have similar $\delta^{13}C$ ratios (Stout et al. 1975, J.H.Troughton, pers. comm.) and may be represented isotopically as a distinct group;
3) the $\delta^{13}C$ of detritus is the same as that of the original plant material (Haines 1977).

In this study, the stable carbon isotope ratios of *Chione* and other members of the macrofaunal community are compared with those of potential food sources to test the hypothesis that terrestrial detrital input (and its associated bacteria) are a significant food source of *Chione* in the AHE.

6.2 Methods

6.2.i. Sample collection and preparation

Samples of *Chione*, other macrofaunal invertebrates and plants were collected from five sites in the AHE representing extremes in hydrological influence (Fig. 6.4):

Site A in the line of discharge from the Bromley oxidation ponds
" B at the mouth of the Heathcote River
" C at the mouth of the Avon River
" D at the estuary mouth (Moncks Bay)
" E in McCormacks Bay

between January 14 and 21, 1980.

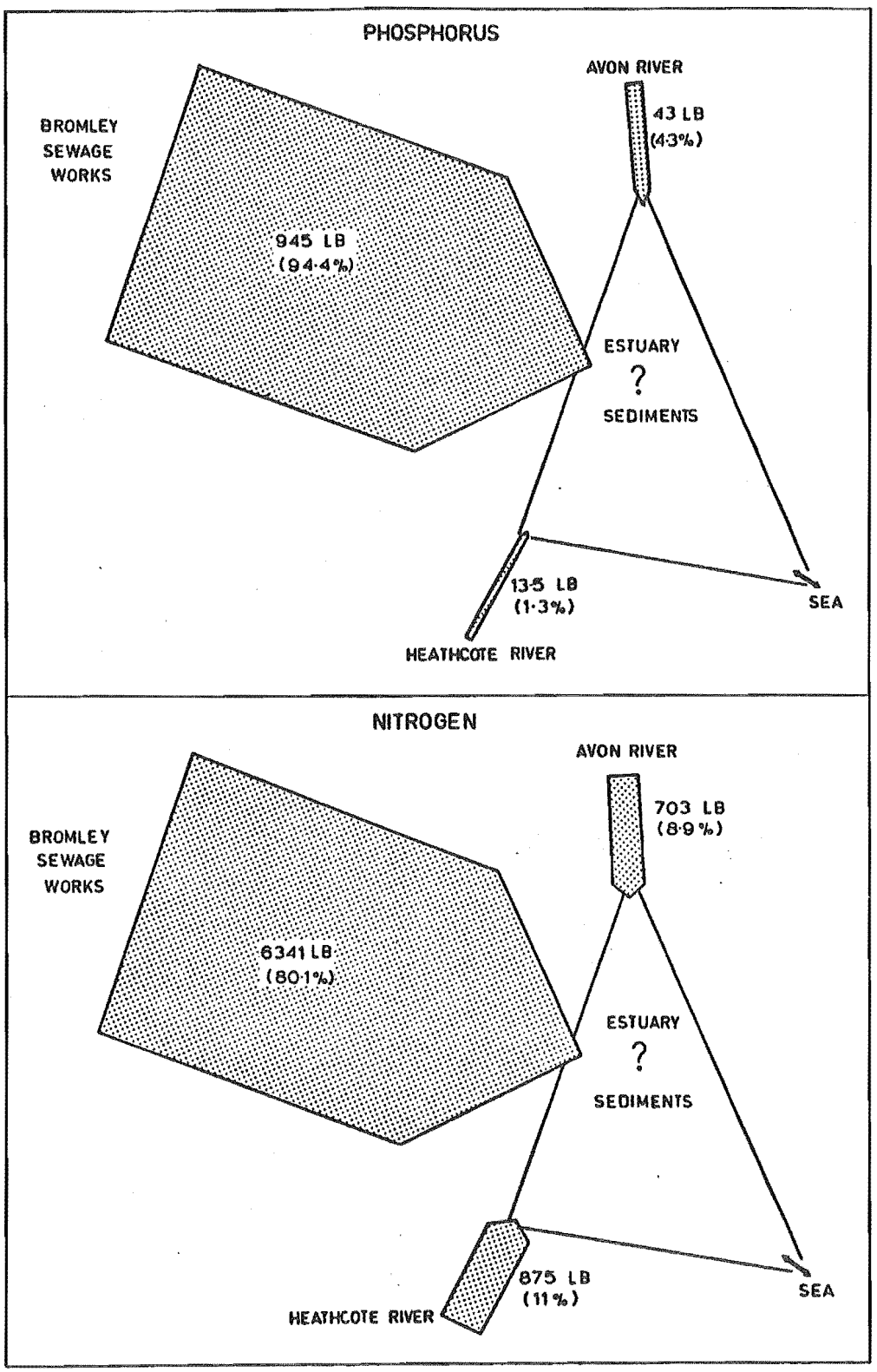


Fig. 6.3 Relative daily contribution of nutrients to the AHE from freshwater sources. After Knox and Kilner 1973: 101.

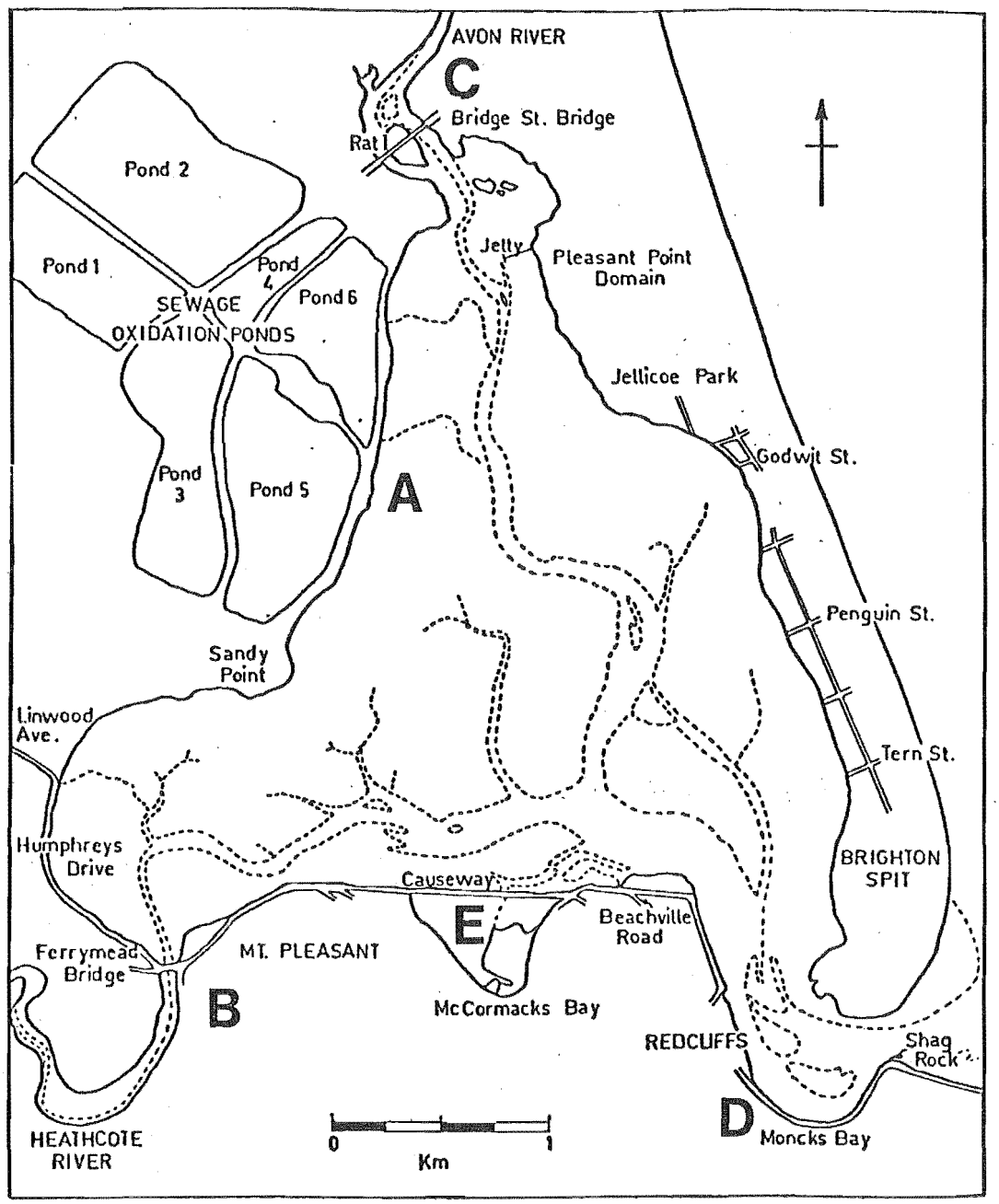


Fig. 6.4 Location of sample sites in the Avon-Heathcote estuary, Christchurch. A, sewage oxidation ponds discharge; B, Heathcote River mouth; C, Avon River mouth; D, Moncks Bay (estuary mouth); E, McCormacks Bay.

Subsamples were preserved intact, and in most cases additional subsamples dissected into body components (such as adductor muscle, foot etc.).

Samples of pectoral muscle were obtained from freshly killed samples of the South Island pied oystercatcher (*Haematopus ostralegus finschi*) and the Eastern bar-tailed godwit (*Limosa lapponica*) on April 2, 1980.

All material was quickly frozen in a blast freezer within a few hours of collection, and stored at -30°C.

Samples of suspended particulate organic matter were collected using a 200 µm mesh diameter plankton net from the oxidation pond discharge and the mouths of the Heathcote and Avon Rivers (sites A, B, C). These were filtered on to pre-combusted glass-fibre filter papers, and both scrapings of residue, and filter papers + residue, frozen.

Plankton samples from the area of ponding (just off the estuary mouth) and from true marine water (2 km off estuary mouth) were collected in 10 minute hauls with the same net on January 25, 1980; and treated in the same manner.

Subsamples of all plankton samples were preserved in (1) Lugols iodide, (2) 10% formalin and (3) permanent slides of filters stained and cleared with Lactophenol PVA, for later identification.

All glassware and utensils were cleaned in chromic acid, and care was taken to avoid contamination of samples.

Frozen samples were freeze dried, capped and stored in a desiccator.

Subsamples of material suspected of containing inorganic carbonates (i.e. crabs, samples with sand in gut, etc.) were treated with a few millilitres of high purity 10% HCl for a minimum of five hours and evaporated to dryness at 50-60°C (Tan and Strain 1979A,B; see also Fry and Parker 1979, McConnaughey and McRoy 1979A,B, Parker et al. 1972).

6.2.ii. Analysis of $\delta^{13}C$

Stable carbon isotope analysis involves three steps; (i) evolution of CO_2 by oxidation of the sample, (ii) purification of the CO_2, and (iii) analysis of the isotopic composition of CO_2 by mass spectrometry. This was carried out at the DSIR Institute of Nuclear Sciences, Lower Hutt, in May 1980, under the direction of Dr G.L. Lyon as follows.

(i) Evolution of CO_2

A break-seal combustion method, similar to that of Buchanan and Corcoran (1959) was used.

Vycor (quartz) glass tubes of 6 mm O.D. were cut to 250 mm length, and one end sealed. 0.8 gm of CuO powder which had been previously heated in a stream of O_2 at 700-800°C was added.

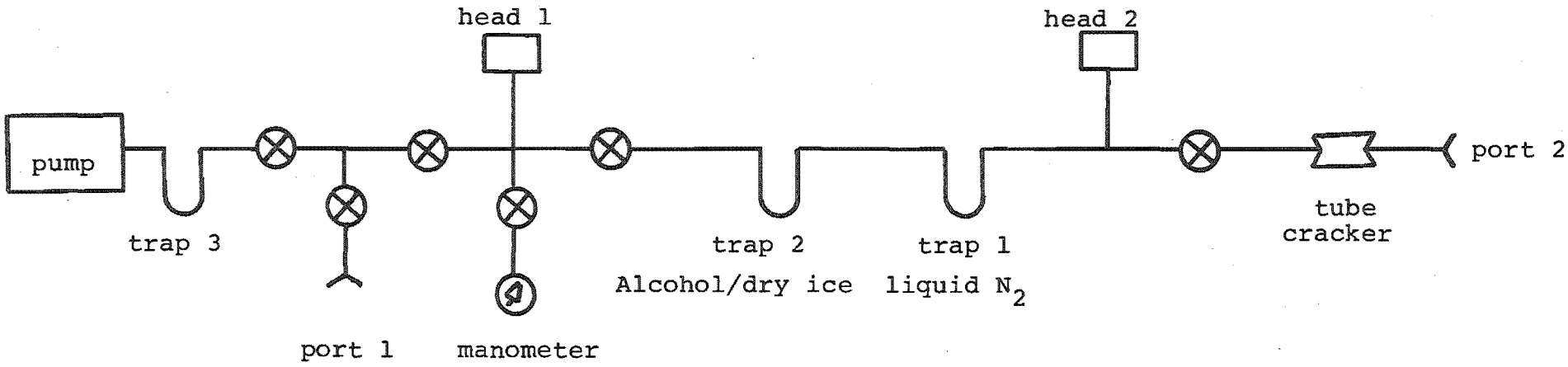


Fig. 6.5 Diagramatic representation of the vacuum line used to purify CO_2

A subsample of 3-5 mg of dry organic matter was weighed into the tube and a clean, reduced (previously heated in a stream of hydrogen at 900°C) silver wire of 50-75 mm added. The tube was evacuated to 0.1 torr for five minutes and sealed. Sets of tubes were heated in a muffle furnace (with the end containing silver slightly raised) to 900%, held at temperature for one hour and allowed to cool overnight.

The CuO and reduced silver wire removed halogen, sulphur and nitrogen compounds (D.J. DesMarais, pers. comm. to G.L.L.), leaving only CO_2, water and some nitrogen gases.

(ii) Purification of CO_2.

Tubes were cracked into a vacuum line (Fig. 6.5) using a Cajon (321-6-X-1) flexible tube cracker. Water was separated by dry-ice + ethanol cooled traps, the CO_2 frozen in a liquid nitrogen trap and the nitrogen gases pumped away.

Yield of evolved CO_2 was measured using a manometer and the sample transferred to a gas bottle.

(iii) Mass spectrometry.

The purified CO_2 was analysed in a Nuclide 6-60 sector, double inlet, ratio mass spectrometer. Sample CO_2 is compared to that of a T.K.L. (Te Kuiti limestone) standard, and $\delta^{13}C$ values calculated according to the method of Craig (1957), with corrections applied for the contribution to mass 45 from ^{12}C, ^{16}O and ^{17}O, and for mass discriminatory effects in the mass spectrometer. The results are expressed as $\delta^{13}C$ with respect to the P.D.B. standard in ‰ (eqn 1, page 2).

6.3 Results

Eighty samples of animal, plant and suspended particulate organic matter were analysed for $\delta^{13}C$ (Table 6.1).

Two batches of CuO were used in the combustion of samples and it became apparent that the "new" batch was contributing to the yield of CO_2 (blanks 6-1, 7-9 and 10-1; Table 6.1). This CuO had been fired in a larger batch and at a slightly lower temperature than the "old" batch. It was also less dense (filled more of the combustion tube) and harder to evacuate.

TABLE 6.1 Stable carbon isotope analysis of animals and plants of the Avon-Heathcote Estuary, carried out at the DSIR Institute of Nuclear Sciences (series R9074). A = acid treated samples; O = "old", N = "new" (poorly fired) CuO.

Sample No.	Tube No.	Sample Description	CuO	$\delta^{13}C_{PDB}$ (‰) uncorrected	corrected
		Moncks Bay			
1	4-1	*Chione*, foot	O		-18.3
1A	4-8	" foot	O		-18.2
2	4-2	" gut and gonad	O		-19.2
2A	4-9	" gut and gonad	O		-19.1
3	4-3	" adductor muscle	O		-17.9
4	1-4	" gills	O		-18.8
4	4-4	" gills	O		-18.9
5	4-5	" siphons	O		-18.4
7	4-6	" digestive diverticulum	O		-20.3
8	4-7	" mantle	O		-18.4
10	5-3	") whole flesh	O		-17.9
11	5-4	") of separate	O		-17.4
12	5-5	") individuals	O		-17.9
15	5-8	" individual foot	O		-18.1
16	5-9	" individual foot	O		-18.3
17	5-10	" individual foot	O		-18.3
18	5-11	" individual foot	O		-18.1
19	5-12	" individual foot	O		-18.6
21	3-1	" foot, low tide	O		-18.1
23	3-2	" foot, mid tide	O		-18.1
25	3-3	" foot, high tide	O		-17.4
27	8-8	*Hemigrapsus crenulatus*, whole	N	-14.21	-15.0
27A	8-9	" " whole	N	-16.52	-17.6
31	8-3	*Cominella maculosa*, foot	N	-14.31	-14.7
		McCormacks Bay			
32	7-8	red alga	N	-13.73	-14.3
33	4-11	green alga (*Enteromorpha ramulosa*?)	O		-13.3
36	8-5	*Mytilus edulis aoteanus*, feet	N	-15.29	-15.9
37	3-4	*Chione*, feet	O		-16.7
39	2-1	*Ulva lactuca*	N	-13.06	-13.5
40	7-2	*Gracilaria secundata*,	N	-12.95	-13.3
41A	8-10	*Hemigrapsus crenulatus*, whole	N	-12.29	-12.5
43	8-4	*Cominella maculosa*, foot	N	-8.82	-8.4
43A	10-10	" " foot	O		-9.9
45	10-5	*C. glandiformis*, flesh	O		-13.1
		Heathcote River Mouth			
47	7-3	*Juncus maritimus*	N	-22.36	-24.3
48A	8-11	*Helice crassa*, whole, from *Juncus* marsh	N	-17.16	-18.4
50	7-4	*Spartina* x *townsendii*	N	-13.69	-14.2
51	7-5	*Ulva lactuca*	N	-12.13	-12.5
52	3-5	*Chione*, feet	O		-21.0
		Avon River Mouth			
56	4-12	*Juncus maritimus*	O		-25.8
57	7-6	*Leptocarpus simplex*	N	-21.85	-23.5
58	4-10	*Zostera muelleri*	O		-18.2
59A	8-12	*Helice crassa*, whole	N	-17.56	-19.1
60	8-6	*Amphibola crenata*, feet	N	-15.92	-16.6
61	7-7	*Spartina* x *townsendii*	N	-12.47	-12.7
63	3-6	*Chiona*, feet	O		-20.6

TABLE 6.1 (Continued)

Sample No.	Tube No.	Sample Description	CuO	$\delta^{13}C_{PDB}$ uncorrected	$\delta^{13}C_{PDB}$ corrected
		Oxidation Pond outfall			
70	3-7	*Chione*, feet	O		-23.5
72	8-8	*Amphibola crenata*, feet	N	-15.52	-16.6
74	9-6	*Euglena* +/or diatoms	N	-15.99	-17.4
74A	9-12	" " (acidified)	N	-17.07	-18.2
65	3-8	discharge residue	O		-22.8
65A	3-9	" "	O		-24.3
65	9-4	" "	N	-19.75	-22.4
65A	9-10	" "	N	-20.00	-24.0
		Heathcote River			
67	9-5	water residue	N	-21.55	-24.9
67A	9-11	" "	N	-22.56	-26.0
		Avon River			
69	9-3	water residue	N	-19.60	-22.2
69A	10-4	" "	O		-24.7
		Marine Plankton			
76	)		O		-18.2
76A	)	outside estuary	O		-18.3
76	)	influence, residue	N	-16.72	-18.2
76A	)		N	-17.69	-18.8
79	9-2)	area of mixing, just	N	-20.48	-22.72
79A	9-8)	off Cave Rock, residue	N	-20.50	-22.51
		Miscellaneous			
83	3-12	Lawn clippings, Zool. Dept, Ilam	O		-28.2
84	8-1	S.Island Pied Oystercatcher, pectoral muscle	N	-15.51	-16.1
90	8-2	Godwit, pectoral muscle	N	-19.39	-20.7
		Winterbourn/Rounick Samples			
J-1	10-6	*Nothofagus* leaves	O		-27.9
J-3A	10-7	*Deleatidium* sp., bodies	O		-29.2*
J-3A	10-8	*Zelandopsyche ingens*, bodies	O		-26.9
J-4A	10-9	*Stenoperla prasina*, bodies	O		-27.3
		Blanks			
	6-1	"New" CuO + Silver, 17 mm yld	N	-11.57	
	7-9	" " " 18 mm yld	N	-11.35	
	8-13	"Old" CuO + Silver, 5.5 mm yld	O		-23.7
	10-1	"New" CuO + Silver, 17.5 mm yld	N	-11.43	
	10-2	"Old" CuO + Silver, 1 mm yld	O		-
		Standards			
	5-2	Bowen's Kale Std (R9091)	N	-26.37	-29.0
	7-12	" " " "	N	-25.45	-28.6
	7-10	Graphite NBS-21 Std (R4389)	N	-25.99	-28.1
	10-11	" " " "	N	-26.02	-28.3
	7-11	Sucrose Std (R4331)	N	-10.67	-10.5

* Some sample lost - result suspect.

As a constant (0.8 g) amount of CuO was used in each sample, the contribution from the CuO was constant, and was corrected for in the following way. The results of three "blanks" using "new" (= poorly fired) CuO are presented in Table 6.2.

TABLE 6.2 Yield and $\delta^{13}C$ values of CO_2 evolved from "new" (= poorly fired) CuO.

Sample	yield (mm)	$\delta^{13}C_{PDB}$
6-1	17	-11.57
7-9	18	-11.35
10-1	17.5	-11.43
Mean	17.5	-11.45

Since the $\delta^{13}C_{PDB}$ value is a more precise measurement than the yield, it is used in Table 6.3 to calculate the theoretical yield derived from CuO according to the equation:

$$\text{true } \delta^{13}C_{PDB} = \frac{\left(\begin{matrix}\text{observed}\\ \text{total yield}\end{matrix} \times \begin{matrix}\text{observed}\\ \delta^{13}C_{PDB}\end{matrix}\right) - \left(\begin{matrix}\text{yield}\\ \text{from CuO}\end{matrix} \times \begin{matrix}\delta^{13}C_{PDB}\\ \text{from CuO}\end{matrix}\right)}{\text{observed total yield - yield from CuO}} .$$

TABLE 6.2 Calculation of the average yield of CO_2 from "New" CuO, based on correction of samples with known $\delta^{13}C_{PDB}$ values *.

Sample		observed total yield	observed $\delta^{13}C_{PDB}$	$\delta^{13}C_{PDB}$ CuO	$\delta^{13}C_{PDB}$ Literature	$\delta^{13}C_{PDB}$ Previous	Calculated CuO yield	Calculated $\delta^{13}C_{PDB}$
NBS 21 Graphite	7-10	120 mm	-25.99	-11.45	-27.85	-27.99[A]	14.5 mm	-27.99
	10-11	112.5 mm	-26.02	-11.45	to -28.19	-27.99[A]	13.4 mm	-27.99
Bowen's Kale (R9091)	5-2	100 mm	-26.37	-11.45		-28.87[B]	14.4 mm	-27.88
	7-12	83 mm	-25.45	-11.45		-28.87[B]	16.3 mm	-28.87
Marine plankton 76	9-1	69 mm	-16.72	-11.45		-18.15[C]	14.7 mm	-18.15
Oxid. discharge residue 65	9-4	63 mm	-19.75	-11.45		-22.83[D]	17.1 mm	-22.84
							Mean=15.1	

A = mean of 11 over 3 months
B = mean of 3
C = sample 3-10
D = sample 3-8

* Sucrose standard was not included because the δ-ratio is too close to that of the "CuO". Samples 76A and 65A are not included because of different acid treatments.

A mean yield of CO_2 of 15.1 mm at a $\delta^{13}C_{PDB}$ of -11.45 was assumed, and used to correct δ-values of those samples with which "New" CuO was used (Table 6.1).

Analytical precision was judged on the basis of eleven replicates of a graphite standard (NBS-21) analysed over a period of three months (G.L. Lyon unpubl. data, R4389). The results (Table 6.4) reveal a mean of -27.99 (standard deviation = 0.117, range = 0.36).

TABLE 6.4 Replicates of the graphite standard NBS-21 analysed over three months.

$\delta^{13}C$	$\delta^{13}C$		
-28.07	-28.11		
-27.80	-28.05	mean $\delta^{13}C$	= -27.99
-28.08	-27.99	S.D.	= 0.117
-27.91	-28.16	range	= 0.36
-27.83	-27.94		
-27.92			

This compares very well with literature values for NBS-21 (-27.79, Craig 1957; -27.85, Lyon and Baxter 1978; -28.19, Mook 1970) and with the precision generally considered feasible in $\delta^{13}C$ analysis (± 0.2‰ DeNiro and Epstein 1978, Rau and Hedges 1979, etc.).

The effect of acid treatment (10% HCl, to remove carbonates) was assessed on a series of samples (Table 6.5).

TABLE 6.5 Comparison of $\delta^{13}C$ values before and after treatment with 10% HCl. H = heavy, L = light.

	Sample	Before acid treatment Sample	$\delta^{13}C_{PDB}$	After acid treatment Sample	$\delta^{13}C_{PDB}$	Shift H/L,
79	Inshore plankton	9-2	-22.7	9-8	-22.5	H 0.2
1	*Chione* foot	4-1	-18.3	4-8	-18.2	H 0.1
2	" gut and gonad	4-2	-19.2	4-9	-19.1	H 0.1
76	Marine plankton	3-10	-18.2	3-11	-18.3	L 0.1
	" "	9-1	-18.2	9-7	-18.8	L 0.6
74	Sediment *Euglena* etc.	9-6	-17.4	9-12	-18.2	L 0.8
67	Heathcote plankton	9-5	-24.9	9-11	-26.0	L 1.1
65	Oxid. pond plankton	3-8	-22.8	3-9	-24.3	L 1.5
	" " "	9-4	-22.4	9-10	-24.0	L 1.6
69	Avon plankton	9-3	-22.2	10-4	-24.7	L 2.5
43	*Cominella* tissue	8-4	-8.4	10-10	-9.8	L 1.4
27	*Hemigrapsus*, whole	8-8	-15.0	8-9	-17.6	L 2.6

Acid treatment made an insignificant difference to samples of *Chione* tissues, but considerable difference to some plankton samples (in which zooplankton exoskeleton was present) and especially to crab body samples.

6.4 Discussion

Although "whole flesh" samples of individual *Chione* from the same area showed little variation in $\delta^{13}C_{PDB}$ (Table 6.6), variation could be expected, especially as a result of undigested food and sediment in the gut of whole animals. Therefore, foot muscle (which can be easily and clearly excised) was used for comparative analysis.

TABLE 6.6 Individual variation in $\delta^{13}C$ of "whole flesh" samples of *Chione* from Moncks Bay.

Sample	$\delta^{13}C_{PDB}$	
10 5-3	-17.9	
11 5-4	-17.4	Mean = -17.7
12 5-5	-17.9	

The variation in $\delta^{13}C_{PDB}$ among individual *Chione* feet from one area is very small (Table 6.7) and the foot is isotopically representative of the muscular parts of the body (Table 6.8).

TABLE 6.7 Variation in $\delta^{13}C_{PDB}$ among individual *Chione* feet: Moncks Bay, low tide.

Sample	$\delta^{13}C_{PDB}$	
15 5-8	-18.1	
16 5-9	-18.3	mean = -18.28
17 5-10	-18.3	S.D. = 0.20
18 5-11	-18.1	range = 0.5
19 5-12	-18.6	

TABLE 6.8 Relative weight and $\delta^{13}C$ of *Chione* body tissues: Moncks Bay, low water, 14/1/80.

Body part	Proportion of dry flesh weight (%)	Sample.	$\delta^{13}C_{PDB}$ (‰)
adductor muscle	16.9	3 4-3	-17.9
foot muscle	7.8	1 4-1	-18.3
mantle	13.3	8 4-7	-18.4
siphons	9.1	5 4-5	-18.4
gills	11.4	4 4-4	-18.8
gut and gonad	29.6	2 4-2	-19.2
digestive diverticulum	11.8	7 4-6	-20.3

The body tissues of *Chione* analysed varied by 2.4‰ (Table 6.8). Muscle was heaviest; gut, reproductive and digestive tissues lighter. The comparatively light value for digestive diverticulum is likely the result of stored biochemical fractions such as glycogen or lipid (see DeNiro and Epstein 1978).

Individual animals of the same species feeding on the same food source should show a small individual variation in $\delta^{13}C_{PDB}$ (Fry and Parker 1979). The extremely small individual variation noted for *Chione* in the same area (Table 6.7) indicates that animals at a particular site in the AHE are utilizing the same food source.

If *Chione* in all parts of the estuary were utilizing the same food source a small spatial range in $\delta^{13}C_{PDB}$ would be expected. However, the foot tissue of *Chione* from five sites differed by as much as 6‰ (Table 6.9). This is too great a range to be accounted for by differences in animal metabolism (DeNiro and Epstein 1978, Teeri and Schoeller 1979) and is attributed in this case to the utilisation of food sources of different isotopic composition.

TABLE 6.9 $\delta^{13}C$ values of *Chione* foot tissue and particulate organic matter ("plankton") at five sites in the Avon-Heathcote Estuary.

	Site	$\delta^{13}C_{PDB}$ *Chione*	$\delta^{13}C_{PDB}$ particulate organic matter + plankton
terrestrial ↑	A Bromley Oxidation Pond Outfall	-23.5	-24.1
	B Heathcote River Mouth	-21.0	-26.0
	C Avon River Mouth	-20.6	-24.7
	D Moncks Bay (AHE mouth)	-18.3	-22.5 (onshore)*
			-18.6 (offshore)*
↓ marine	E McCormacks Bay	-16.7	

* "onshore" is a mixture of marine and estuary water; "offshore" is true marine water.

Isotopic values of suspended particular matter and "plankton" sources in the AHE are shown in Table 6.9. True marine ("offshore") has a $\delta^{13}C$ value of -18.6. Since an animal assumes a $\delta^{13}C$ value slightly heavier than that of its food (DeNiro and Epstein 1978, etc.), the *Chione* of Sites A, B and C ($\delta^{13}C$ values -20.6 to 23.5) could not have been utilizing only marine derived particulate matter but must have had a much lighter food source (at least -20.6 to -23.5‰). This food source is undoubtedly the particulate matter of inflowing freshwater sources (range -24.1 [Bromley oxidation ponds] to -26.0 [Heathcote River]) much of which is of terrestrial origin.

Chione at site A reflect well the dominant energy flow contributed by Bromley Ponds with a $\delta^{13}C$ ratio almost that of the inflowing particulate matter. Animals from the two rivers have ratios between that of the river particulate matter and that of marine matter - indicating utilization of both sources. On the other hand *Chione* from Moncks Bay reflect predominantly marine influence with a $\delta^{13}C$ value very near that of marine plankton.

Chione of McCormacks Bay are considerably "heavier" than marine plankton. This isolated bay (which because of altered drainage only receives water at high tide, and is very saline) supports very dense blooms of algae, especially *Ulva* and *Gracilaria*; both of which have $\delta^{13}C$ values of about -13.3 (Table 6.10).

TABLE 6.10 $\delta^{13}C$ values of *Chione*, and algae from McCormacks Bay, and marine plankton (‰).

marine plankton	-18.6
Chione tissue	-16.7
algae - *Ulva*	-13.5
Gracilaria	-13.3

It is probable that the *Chione* of this bay are utilizing some algal detritus. The tendency to a heavier ratio in McCormacks Bay is evident in other animals (Table 6.11). Thus, the bay represents the most marine extreme in the AHE system.

TABLE 6.11 Comparison of $\delta^{13}C$ values of *Chione*, *Hemigrapsus* and *Cominella maculosa* from Moncks Bay and McCormacks Bay.

Animal	D) Moncks Bay	E) McCormacks Bay
Chione	-18.3	-16.7
Hemigrapsus	-17.6	-12.5
Cominella maculosa	-14.7	-9.8

An influence of tidal position was noted in *Chione* at Moncks Bay (Table 6.12). *Chione* at high tide had a heavier ratio than those at mid and low tide. Animals high on the shore would be covered (and therefore feeding) only about maximum tide - when most sea water is present - and would be expected to reflect a more marine contribution.

Table 6.12 Tidal variation in $\delta^{13}C$ of *Chione* feet from Moncks Bay. (Pooled feet of 5 individuals from each level.)

Tide level	$\delta^{13}C$
High	-17.4
Mid	-18.1
Low	-18.1

From these data, it may be concluded that *Chione* is an indiscriminate filter feeder, feeding on particulate organic matter of terrestrial (site A), marine (site D) and estuarine (site E) origin depending upon its position within the estuary. Clearly the relative proportions of each of these inputs to *Chione* at a certain site would be directly related to local hydrological characteristics.

Although spatial gradients in $\delta^{13}C$ associated with marine and terrestrial origin of the food source have been shown in communities (different species) and in one species over a large area (Fry and Parker 1979), it has not been previously demonstrated in one species in such a small area.

7. FUTURE OF $\delta^{13}C$ STUDIES

1. Elucidation of food webs

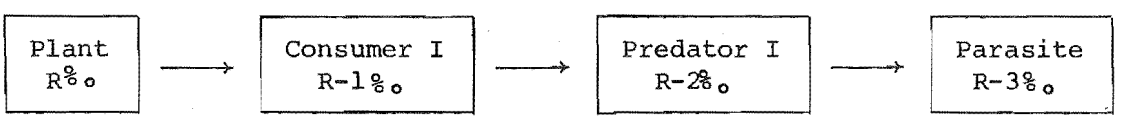
The use of stable carbon isotopes as natural tracers in the study of food webs appears very promising for many ecological systems. This will be especially true when the number of carbon sources in a system are small, and these sources are isotopically distinct (Rau 1980).

Since the isotopic record is bound into organic matter with little apparent change by death and decay (Smith and Epstein 1970, Haines 1977), the application of isotopic analysis to organic matter long dead, or even fossil matter, may reveal useful information about the environment or metabolism of the organism (Wickman 1952, Troughton, Wells and Mooney 1974, Stout et al. 1975, Smith and Epstein 1976, DeNiro and Epstein 1978, G.H. Rau pers. comm.).

2. Estimating carbon cycling

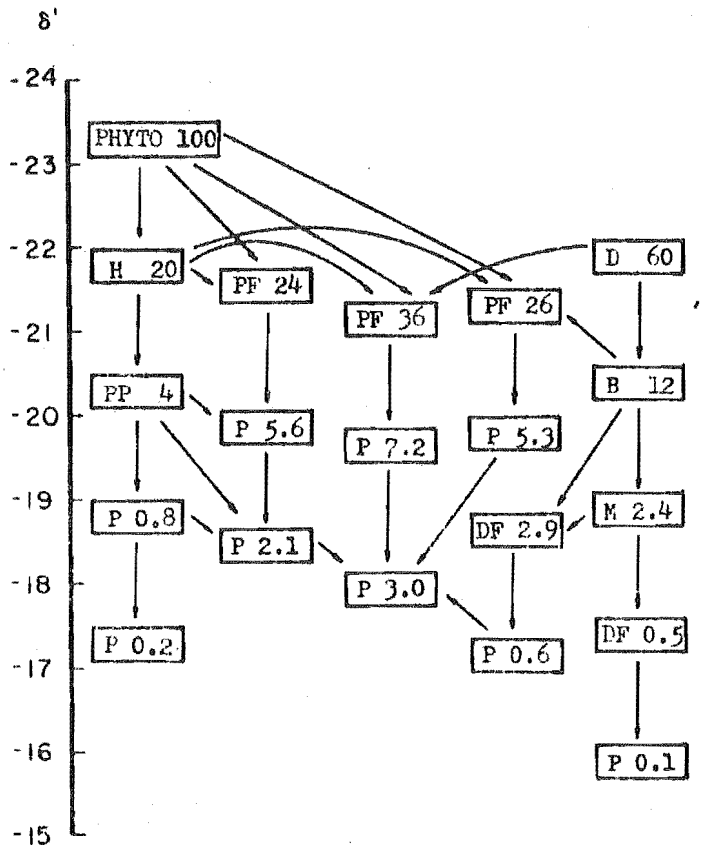
Another major area of advancement for isotope analysis may be estimation of the amount of "processing" of carbon in a system. ^{13}C undergoes modest "biomagnification" in the food web, apparently as a result of being respired at a lower specific rate than ^{12}C (McConnaughey and McRoy 1979A). Theoretically then, the magnitude of the difference between the isotope ratio of a consumer trophic level and its ultimate food source will reflect the number of times the original carbon has been processed (see 7.3).

For example, given the approximate enrichment of an animal compared with its food of 1‰ (DeNiro and Epstein 1978, and others) a sequence such as the following would be expected:



where R is the $\delta^{13}C$ value. McConnaughey and McRoy (1979A) present a model marine food web based on one carbon source (Fig. 7.1).

Rau (1978) in a study of a subalpine lake noted that plankton $\delta^{13}C$ (-45‰) was far too light to be accounted for by normal one-step fractionation of atmospheric CO_2 (-7‰) through aquatic plants (normally -10 to -30‰); and suggests that biogenic (respiration) CO_2 (from sediment respiration, etc.), depleted in ^{13}C was an important component of the inorganic carbon used to produce the organic plankton. Lowered inorganic $\delta^{13}C$ as a result of the addition of biogenic CO_2 has been noted in air (Keeling 1958), lakes (Oana and Deevey 1960), soils (Galimov 1966), sea water (Deuser and Hunt 1969, Tan and Strain 1979B), and brackish water (Mook 1970).



Distribution of carbon isotopes in a model marine food web. Each component of food web (represented by a box) has a corresponding $^{13}C:^{12}C$ ratio (ordinate) and a number representing the efficiency with which phytoplankton carbon is converted into that component (number inside box). Feeding relations are shown by arrows, and a general description of each component is suggested by abbreviations inside boxes. PHYTO: phytoplankton; H: herbivore; PF: particle feeder; PP: pelagic predator; P: predator; D: detritus; B: bacteria; M: meiofauna; DF: deposit feeder

Fig. 7.1 Distribution of carbon isotopes in a model marine food web based on one carbon source. From McConnaughey and McRoy 1979A: 261.

In cases where a consumer trophic level is removed physically or in time from its food source, stable carbon isotope ratios may give an indication of the nature and degree of carbon cycling between the two.

Two possible examples of such systems may be:

1) the degree of processing of beech leaf carbon by bacteria before it is assimilated by stream invertebrates (M.J. Winterbourn and J. Rounick, pers. comm.)

2) the origin and degree of processing of organic carbon in the under-ice ecosystem of the Ross Sea (G.A. Knox, pers. comm.).

3. Animal energetics

A very exciting prospect is the analysis of $\delta^{13}C$ in components of animal energy budgets.

The carbon budget of an individual may be represented, in terms of isotope ratios, as in Fig. 7.2.

In an excellent paper, McConnaughey and McRoy (1979A) point out that because isotopes are conserved in metabolism, the extent of ^{13}C enrichment in a consumer (compared to its food) must reflect the carbon budget of the consumer

$$Y = \frac{\text{respiration}}{\text{assimilation}} = \frac{R(\text{food}) - R(\text{consumer})}{R(CO_2) - R(\text{consumer})}$$

where R represents the $^{13}C:^{12}C$ ratio, and
Y represents the ratio of respiration to assimilation.

By rearrangement; a consumer will be ^{13}C enriched compared to its food by the factor

$$g = \frac{R(\text{consumer})}{R(\text{food})} = \frac{1 - Y[R(CO_2) / R(\text{food})]}{1 - Y} \quad .$$

The consumer will therefore be most enriched in ^{13}C if it respires much of the carbon it assimilates (Y is large) and if each consumer increases the $^{13}C:^{12}C$ ratio by some factor, gi, the nth consumer in a food chain will have the ratio

$$R_n = R_o\, g_1\, g_2\, g_3 \cdots g_n \quad ,$$

(where R_o is the $^{13}C:^{12}C$ ratio of primary production).

If g is constant, then $R_n = R_o(g)^n$ and the "trophic level" (n) can be defined as

$$n = \log (R_n/R_o) / \log(g) \quad .$$

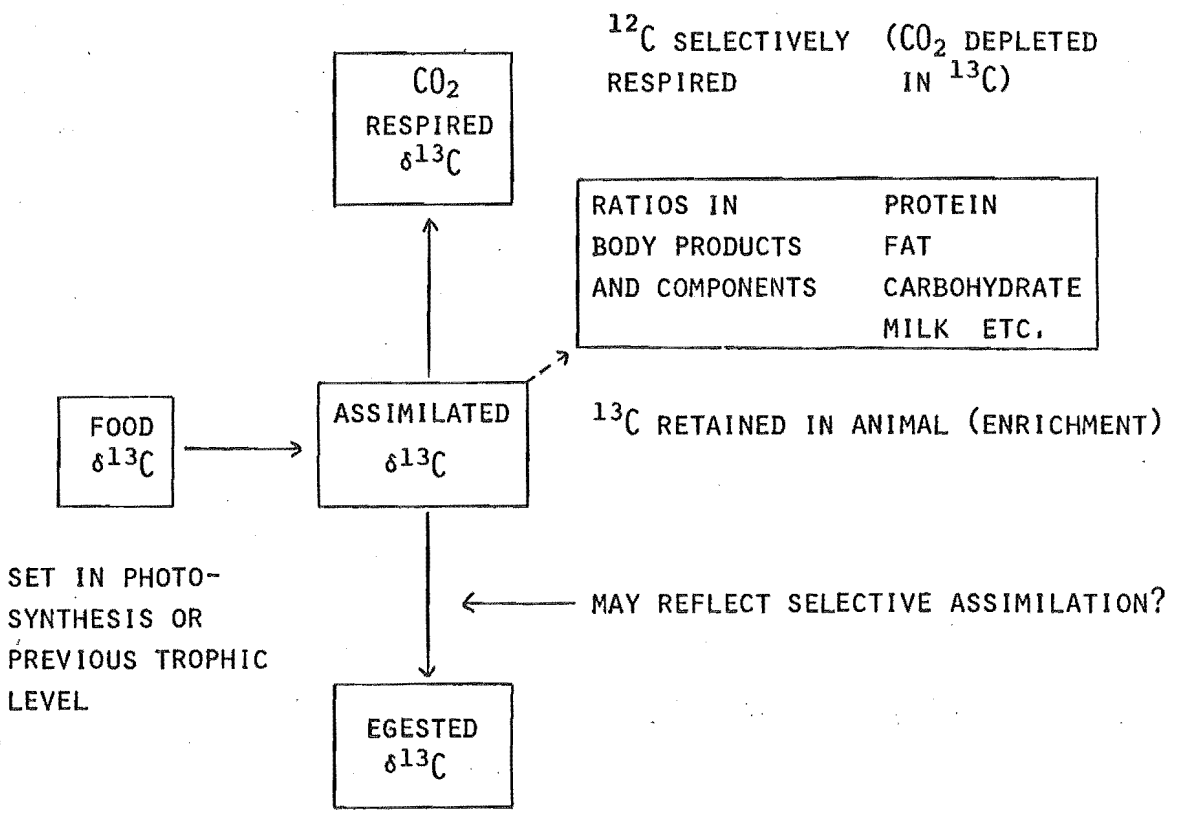


Fig. 7.2 The carbon budget of an individual animal, in terms of isotope ratios.

While this equation underestimates trophic level if an average value of g is used, it provides a parameter for comparing the effective lengths of the food web supporting various animals. Since isotopic enrichment is caused by respiration, n reflects the cumulative respiration which has occurred between photosynthetic fixation of the ratio in primary production, and collection of the animal; or the inefficiency of the food web (McConnaughey and McRoy 1979).

A few studies contain data which indicate that the application of stable carbon isotope analysis to the study of animal and community energetics may be a profitable line of investigation. In a series of papers, Duchesne and co-workers have shown that CO_2 respired by man and dogs differed by only 1.5‰ (Duchesne and Van de Vorst 1968); birds show a similar small difference from mammals while CO_2 respired by frogs had much less ^{13}C than did mammals or birds (Duchesne et al. 1968A); and that diet and metabolism may influence $\delta^{13}C$, by inducing $^{13}C/^{12}C$ changes in respired CO_2 of chickens (with insulin injections; Duchesne et al. 1968B), and in rats (with hormones; Mosora et al. 1971B) (see also Lacroix et al. 1971, Mosora et al. 1971A).

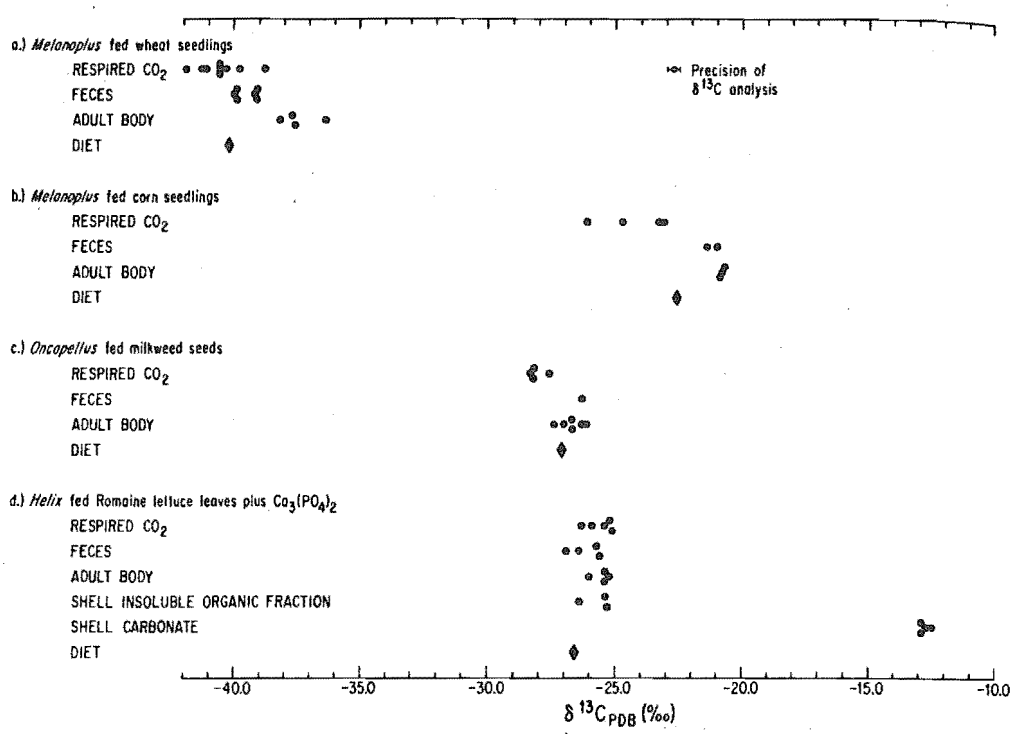
Minson et al. (1975) stated that it should be possible to calculate the proportion of carbon in animal products (such as milk of cattle in their case) coming from feed and from body reserves, or to determine the rate of exchange of body protein and fat by monitoring an animal after a sudden change from one diet (i.e. C_3 pasture) to an isotopically different one (C_4 pasture.

DeNiro and Epstein (1978) analysed the $\delta^{13}C$ values of the input and output components of four animals (Fig. 7.3). They noted that whole body ^{13}C enrichment of (laboratory reared) animals is usually balanced by ^{13}C depletion of respired CO_2, and show this in a mass balance table for the grasshopper *Melanoplus* (Table 7.1).

TABLE 7.1 Isotopic mass balance for *Melanoplus* fed wheat seedlings; from DeNiro and Epstein 1978: 500.

Component	Total weight for five-day period[a] (in mg.)	Carbon concentration[b] (in μ moles CO_2 $mg.^{-1}$)	Total carbon for five-day period (in μ moles CO_2)	$\delta^{13}C_{PDB}$ (‰)
Input				
Food (wheat seedling)	148.0	34.5	5106	-40.2 ± 0.8
Output				
Respired (carbon dioxide)	not determined	---	1378[c]	-40.8 ± 0.6
Excreted (feces)	112.5	30.3	3409	-39.5 ± 0.4
Incorporated (whole body)	8.1	39.4	319	-37.5 ± 0.8
Total (calculated)	---	---	5106[c]	-39.7 ± 0.3

[a] Data of SMITH (1959) for *Melanoplus bilituratus* adults.
[b] Average yield for samples from Fig. 5a.
[c] Calculated by assuming amounts of input and output carbon were equal.



$\delta^{13}C$ values of the input and analyzed output components of four animals. For *Helix*, uric acid and the slime laid down to aid in locomotion were not analyzed. Each point represents the analysis of the specified output component of a single animal, except for the feces (the output of several animals during one day was combined) and the respired CO_2 of *Oncopeltus* and *Helix* (the output of several animals was collected).

Fig. 7.3 $\delta^{13}C$ values of energetic components of four animals; from DeNiro and Epstein 1978: 500.

As well as providing potentially valuable energy budget information (including parameters traditionally hard to quantify such as assimilation and respiration) this line of research would enable clarification of many questions fundamental to the use of $\delta^{13}C$ in food web studies (including the degree to which seasonal, life history stage, and individual variation may influence $\delta^{13}C$).

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4.8.3 Energetic Considerations of Feeding

Population assimilation can be calculated either as

$$A = C - (F+U)$$

or as;

$$A = P + R.$$

The apparent simplicity of measuring energy flux in terms of consumption minus rejecta (C - (F+U)) is deceptive and in most ecological studies, assimilation is calculated as the sum of production and respiration (Richardson, 1975 a, b). Petrusewicz & Macfadyen (1970) point out that field measurements of production are usually more accurate than information from laboratory feeding studies and Phillipson (1967) discusses errors in laboratory feeding studies. As in respiration measurements, problems exist in the inability to reproduce field conditions in the laboratory (Macfadyen, 1967) and the applicability of laboratory measured feeding rates is limited.

No measurements were made of the volume of ingested or egested matter in this study; however estimates were made from literature values.

In spite of differencesin the rates of water transport by bivalves under different experimental conditions, it appears that when related to flesh weight, species fall into two groups with different weight specific rates of water movement (Foster-Smith, 1975). Jorgensen (1966) suggested that burrowing bivalves have low rates (compared with epifaunal, non-burrowing forms) and this is supported by studies on *Mya arenaria* (Allen, 1962; Winter, 1969), *Mya truncata* (Winter, 1969), *Venus striatula* (Allen, 1962), *Venus mercenaria* (Rice & Smith, 1958), *Cerastoderma edule* and *Venerupis pullastra* (Winter, 1969).

Weight specific filtration rates of a number of species from a variety of studies are summarised by Foster-Smith (1975), and range from 0.03 to 10 l hr^{-1} g^{-1}. Burrowing, infaunal species seem to have rates generally between 0.03 and 1.0 l hr^{-1} g^{-1}. Applying this latter range to the population of *C. stutchburyi* in the Avon-Heathcote Estuary results in an estimated volume of water transported by the cockle population of 2.2×10^{7} to 1.5×10^{10} l hr^{-1} filtered, and an estimated time for the population to filter the volume of Avon-Heathcote Estuary water of 0.6 to 375 hours.

Particulate matter filtered from the current of water passing the gills is sorted and either ingested or bound into mucous strings and expelled as pseudofaeces through the inhalent siphon in a temporary reversal of the current, or between the valves near the foot. Of the ration ingested, some is assimilated and the rest egested as faeces (also bound in mucus) via the exhalent siphon. The bundles of faeces and pseudofaeces settle onto the sediment (process of biodeposition).

In winter, no linear shell growth or weight gain occurs in *C. stutchburyi* (Larcombe, 1971) and assimilation is equal to the sum of metabolic activity (R + U). The major expenditure of energy is in respiration, and R is assumed to account for almost all material assimilated and to be approximately equal to 8 J g^{-1} (AFDWt) hr^{-1} (section 4.6).

In summer however, gonad production (Pr) and growth of shell and flesh (Pg) occur; and A = P + R + U (see section 4.9).

Total consumption (C) is higher than A by the amount not assimilated (faeces). This is assumed to be less than 6% of the body weight per day (as calculated by Day *et al.* (1973) for oysters).

Pseudofaecal production in bivalves has been found to vary with concentration of suspended matter. Tenore & Dunstan (1973) noted a logarithmic increase in biodeposition with increasing food concentration and Foster-Smith (1975) found pseudofaecal production of up to 50% of that ingested at high food concentration. Day *et al.* (1973) assumed pseudofaecal production to equal faecal production in oysters.

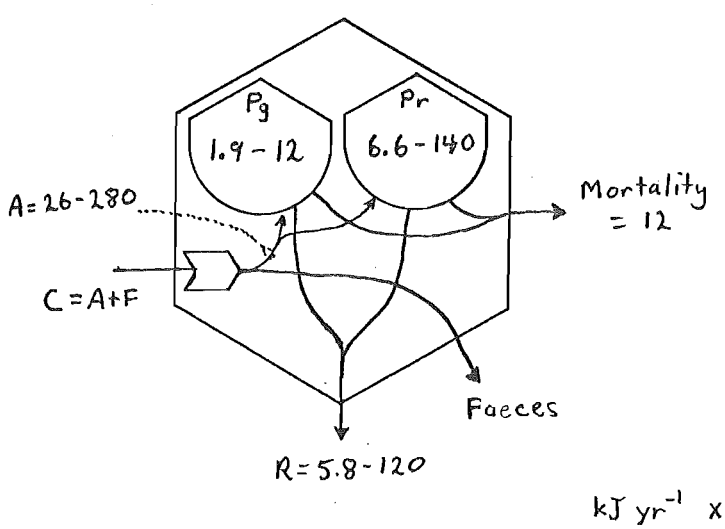
4.9 SUMMARY OF THE BUDGET

An annual energy budget for *C. stutchburyi* in the Avon-Heathcote Estuary is summarised in Table 4.7. Total production is estimated to be between 2.0×10^9 and 1.6×10^{10} kJ yr^{-1}, from a total winter biomass (AFDWt) of 8.2×10^7 to 1.7×10^9 g. Therefore the calculated P/B ratio lies between 24.4 and 9.4 for minimum and maximum estimates of measured population parameters respectively.

Production varies on an areal basis, not only because of variability in density and biomass, but also because of differences in growth rate and age structure of the population. Larcombe (1971) in his study of several populations throughout the species range in New Zealand found that production of *C. stutchburyi* flesh averages 19% of the winter standing crop per year.

Table 4.7 Summary of the total energy (kJ yr^{-1}) in organic production and respiration of *C. stutchburyi* from the Avon-Heathcote Estuary.

Parameter		Energy (kJ yr^{-1})
Production		
P_g	body growth	1.9×10^8 - 1.2×10^9
	(available flesh	7.2×10^7 - 4.6×10^8)
P_r	reproduction	6.6×10^8 - 1.4×10^{10}
M	mortality	1.2×10^9
	(total production	2.0×10^9 - 1.6×10^{10})
Respiration		5.8×10^8 - 1.2×10^{10}
Assimilation = Production + Respiration		2.6×10^9 - 2.8×10^{10}



Larcombe (1971) estimated production values for several Avon-Heathcote sites (Table 4.8) based upon dry weight values assigned to the length/age/frequency characteristics of the population. The "Spit" population (near the experimental plots of this study) with a production of 193.5 g (dry wt) yr^{-1} was the highest recorded from any site in his study. The range of production values calculated by Larcombe are within those calculated in this study, expressed on an areal basis (Table 4.9).

Table 4.8 Production values of *C. stutchburyi* from the Avon-Heathcote Estuary obtained by Larcombe (1971; Table 18.2, p. 170).

Area	No. m^{-2}	Winter standing crop g dry wt	Prod. g dry wt/yr	$\frac{\text{Prod.}}{\text{standing crop}} \times 100$	Prod. k cal	× 4.187 = kJ
spit	1532	777	193.5	24.9	841.7	3.5×10^3
mouth	644	351	45.9	13.1	199.4	8.3×10^2
2C	2508	118	35.2	29.8	153.1	6.4×10^2
3D	2592	132	69.9	53.0	303.2	1.2×10^3
4C	84	16.3	4.6	28.1	20.0	83.7

Table 4.9 Production values of *C. stutchburyi* from the Avon-Heathcote Estuary, expressed on an areal basis (area of cockles = 4.6×10^6 m^2).

Source	Parameter	Production	
		Minimum	Maximum
Table 4.2	Total winter biomass (g AFDWt)	17.8	369.6 g m^{-2}
	Total energy	3.5×10^2	7.4×10^3 kJ m^{-2}
Table 4.3	Yearly net organic production	2.1	13.5 g m^{-2} yr^{-1}
	Yearly energy in net organic production	41.9	260.9 kJ m^{-2} yr^{-1}
Table 4.7	Total yearly production (P + R)	434.8	3.5×10^3 kJ m^{-2} yr^{-1}

5 ENERGY FLOW IN THE AVON-HEATHCOTE ESTUARY

5.1 A GENERAL MODEL

The energy flow parameters of *C. stutchburyi* populations estimated in section 4 give little indication of the significance of this species in the total energy flux of the system, without comparison with energy flow through the estuary as a whole. In this section energy flows are calculated for the Avon-Heathcote Estuary (section 5.1) and these calculations are used to quantify the proportion of the total energy flow related to the cockle (section 5.2) to test the hypothesis that energy flow through *C. stutchburyi* is significant in terms of the total estuary.

Representation of an entire ecosystem in measurable and comprehensible terms requires some degree of simplification; and any attempt to summarise characteristics is essentially modelling.

Recently the concept of energy analysis (the modelling of systems based on a framework of energy flow) has been developed by H.T. Odum (H.T. Odum, 1971a, 1972, 1975, 1978, in press; H.T. Odum & E.C. Odum, 1976) and applied to many ecological systems in order to compare systems and to evaluate the role that parts of the system play in maintaining the whole ecosystem.

Energy analysis involves the synthesis of ecosystem components into a web where energy flow is used as the common unit of measurement among parts. While exchanges in matter and information are also necessary to define the full set of phenomena, the balance of energy flows offers a convenient starting point for consideration of trophic groupings and provides the most obvious manifestation of compliance with thermodynamic principles (Ulanowicz & Kemp, 1979).

It has been applied to a variety of systems for several purposes including documentation of environments, environmental impact statements, and even in attempts to equate physical, biological and socioeconomic components of ecosystems (see especially H.T. Odum, 1971b, 1978, in press; Janssen & Zucchetto, 1978).

The coastal marine ecosystem has received considerable attention and energy analysis has been used to assess specific management alternatives (see reviews by H.T. Odum *et al.*, 1977; Nixon & Kremer, 1977; McKellar, 1977).

A real benefit of energy analysis is in its application to assessment of alternatives in management projects. A few examples (outlined by H.T. Odum *et al.*, 1977) include the assessment of energy flows in converting tidal energy at La Rance, France to electric power; evaluation of water cooling alternatives and impact on the estuarine environment at Crystal River, Florida (H.T. Odum *et al.*, 1975; Smith, 1976; McKellar, 1975); waste treatment and natural recycling (Mitsch, 1975); assessment of aquaculture propositions in a coastal oyster fishery (Boynton, 1975); and evaluation of housing density in coastal areas (Stellar, 1975; Boynton, 1975).

In this study, energy analysis is used to create a framework of the entire Avon-Heathcote Estuary in energy terms, with which data for *C. stutchburyi* may be evaluated.

The first step in energy analysis is the construction of an overview of the system using energy language diagrams. Symbols representing units and processes of the system are connected with pathways representing the flows of energy from sources outside the selected boundaries, through the web of the system, and finally out as degraded, used energy. Basic symbols are shown in Fig. 5.1 and full details are available in H.T. Odum, 1971a, b, 1972, 1975; H.T. Odum & E.C. Odum, 1976; Hall & Day, 1977).

The system boundaries are identified (in this case the physical boundaries of the Avon-Heathcote Estuary) and external sources of energy listed (Fig. 5.2). This list of energy sources acting upon the system is known as the "energy signature" of the system (H.T. Odum & E.C. Odum, 1976).

Following energy flow from these sources through the major functional components results in the formation of a web (Fig. 5.3). This model summarises energy flow through the entire estuary and illustrates the paths of energy that interact with, and must be assessed when considering, any unit of the system.

Basic energy diagrams carry both an energetic and mathematical meaning and as such are models of the system. From such models, subsystems may be extracted and simulated on a computer (section 5.2) using difference equations. Inflows of energy balance outflows and storage according to the first energy law, and all components or interactions have at least a small energy component which is lost (to the "heat sink") according to the second energy law.

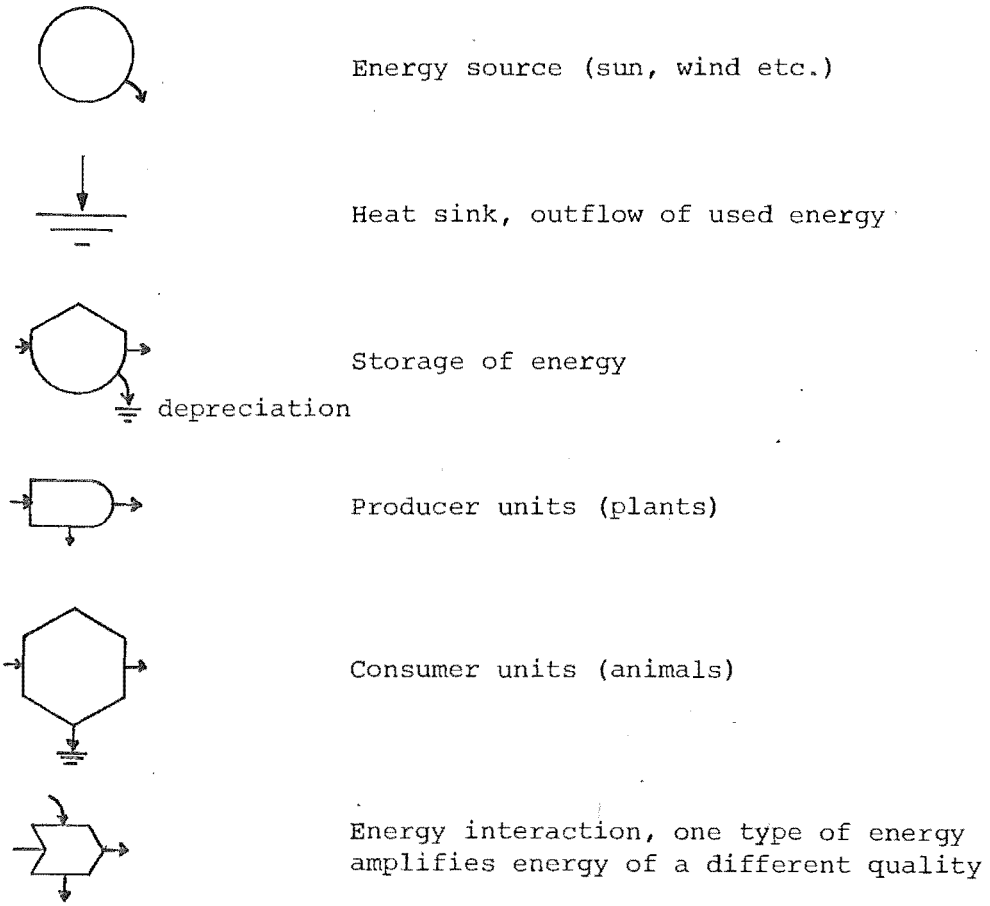


Fig. 5.1 Energy symbols (after H.T. Odum & E.C. Odum, 1976).

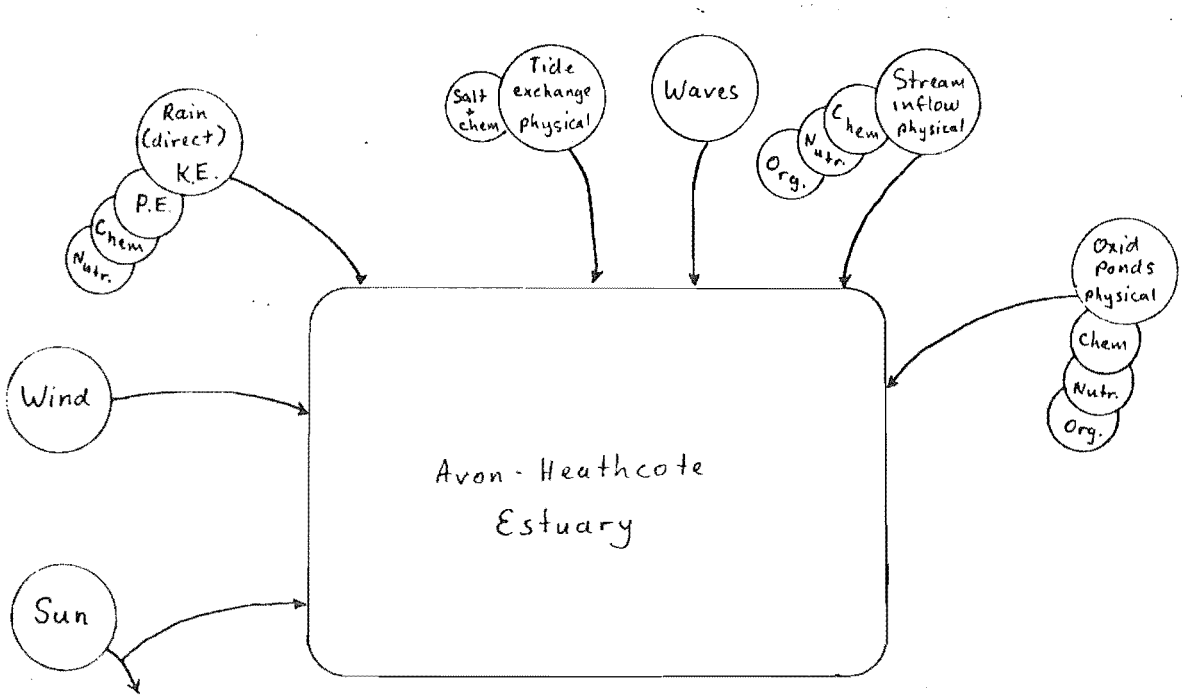


Fig. 5.2 Energy signature of the Avon-Heathcote Estuary.

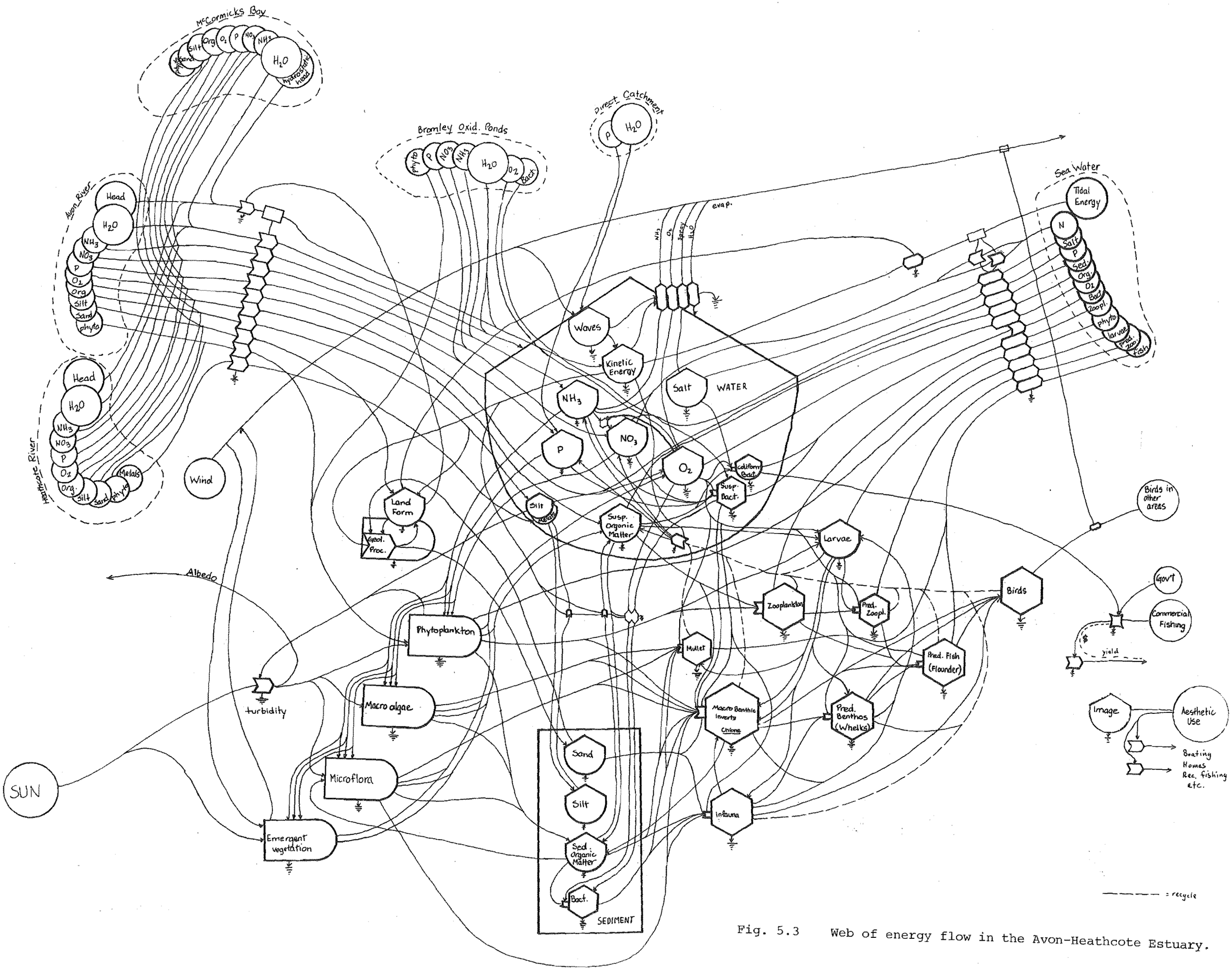


Fig. 5.3 Web of energy flow in the Avon-Heathcote Estuary.

In order to be able to use energy flow diagrams for simulation or empirical modelling, the energy values of the components and flows present must be evaluated. Energy analysis was undertaken on the energy contributions from outside the Avon-Heathcote Estuary, and the results are summarised in Table 5.1.

The pathways of an energy diagram describing a system initially are calculated in energy flow units of different types (energy of sunlight, wind, tide, etc.) and strictly cannot be equated. However, they may be converted to equivalents of one type of energy according to the concept of embodied energy (H.T. Odum, 1978). The energy transformation efficiency, or quality factor, is the energy of one type required through processing to develop flow of another type of energy; for example, the sunlight required to develop plant matter is the embodied energy of that plant matter in solar equivalents (joules of sunlight required). Each pathway then shows the energy required for its development. The idea is simple but calculations are often very approximate and not easily conceptualised, especially when the process passes through a web of feedbacks. At this early stage in energy analysis, calculations are made objectively and documented with the hope that tables of conversion efficiency will be improved with time (H.T. Odum & E.C. Odum, 1980). The quality factors used in this study are taken from H.T. Odum *et al.* (1978).

Pathways expressed in the same units (solar equivalents in this case) may be compared directly; those with the greater energy requirements being most significant.

The total energy acting on the Avon-Heathcote Estuary from external sources was estimated to be approximately 8.1×10^{9} kJ m^{-2} yr^{-1} and in solar equivalents, 3.0×10^{14} kJ_{SE} m^{-2} yr^{-1}.

Physical energy in flows of fresh water and the tide is most significant, followed by nutrient input from the Bromley ponds, and the chemical energy of sea water dilution by fresh water.

5.2 SIMULATION OF ENERGY FLOW THROUGH *C. STUTCHBURYI*

The compartments and paths of energy flow relating to the cockle (investigated in sections 2, 3 and 4) are summarised in Fig. 5.4. *C. stutchburyi* is a dominant member of the benthic macrofauna (section 2) whose distribution is limited by tide and sediment characteristics (2.3). It is a filter feeder, assimilating suspended organic matter of terrestrial, marine, and estuarine origin (4.8.2) and it passes organic

Table 5.1 Energy contributions to the Avon-Heathcote Estuary.

Flow	Heat equivalents ($kJ\ m^{-2}\ yr^{-1}$)	Quality factor	Solar equivalents ($kJ_{SE}\ m^{-2}\ yr^{-1}$)	Note
Solar input	4.97×10^5	1	4.97×10^5	1
Wind	2.2×10^4	315	7.0×10^6	2
Rain (direct catchment)				
kinetic energy	16.0	2.38×10^5	3.18×10^6	3
gravitational potential	8.4	4.0×10^3	3.36×10^4	4
chemical potential	2.7×10^3	6.9×10^3	1.86×10^7	5A
nutrient potential				6A
phosphorus	1.6×10^{-3}	5.2×10^9	8.6×10^6	
nitrogen	6.3×10^{-3}	5.8×10^8	3.7×10^6	
total			1.23×10^7	
Tide energy				
physical	4.26×10^6	3.4×10^3	1.4×10^{10}	7
chemical	Considered in freshwater inputs			
Waves	3.1×10^3	5.1×10^4	1.6×10^8	9
River flow				
physical	6.9×10^9	3.7×10^4	2.6×10^{14}	8A
chemical	3.2×10^5	6.9×10^3	2.2×10^9	5B
nutrient				6B
nitrogen	1.3	5.8×10^8	7.5×10^8	
phosphorus	3.6×10^{-3}	5.2×10^9	1.9×10^7	
total			7.7×10^8	
Oxidation pond discharge				
physical	1.2×10^9	3.7×10^4	4.4×10^{13}	8B
chemical	9.4×10^4	6.9×10^3	6.5×10^8	5C
nutrient				6C
nitrogen	42.9	5.8×10^8	2.5×10^{10}	
phosphorus	2.7	5.2×10^9	1.4×10^{10}	
Total	$8.1 \times 10^9\ kJ\ m^{-2}\ yr^{-1}$		$3.0 \times 10^{14}\ kJ_{SE}\ m^{-2}\ yr^{-1}$	

Footnotes to Table 5.1

1) Solar input

Langleys day^{-1} = 100 (winter)
600 (summer) (Knox & Kilner, 1973)

1 langley = 10 kcal m^{-2} = 11.87 kJ m^{-2}

∴ Winter input = 100 langleys × 41.87 = 4187 kJ m^{-2} dy^{-1}
Summer input = 600 langleys × 41.87 = 25122 kJ m^{-2} dy^{-1}

Mean input = 325 langleys × 41.87 = 13608 kJ m^{-2} dy^{-1}

365 days yr^{-1} = 4.97×10^6 kJ m^{-2} yr^{-1}

Albedo

Assuming albedo = 0.1 then absorbed solar input = 4.97×10^5 kJ m^{-2} yr^{-1}

Quality factor

by definition = 1

therefore 4.97×10^5 kJ_{SE} m^{-2} yr^{-1}

2) Wind energy

Hubbard (1971) lists a mean heat equivalent for winds and storms of the biosphere of 61.1 kJ m^{-2} dy^{-1}.

In the case of the Avon-Heathcote Estuary (6×10^6 m^2 area) wind energy would be approximately (61.1 kJ m^{-2} dy^{-1}) (365 days yr^{-1}) = 2.2×10^4 kJ m^{-2} yr^{-1}.

Quality factor for wind = 315 Solar kcal $kcal^{-1}$ (H.T. Odum, 1978)
therefore solar equivalents of wind energy

= $2.2 \times 10^4 \times 315$ = 7.0×10^6 kJ_{SE} m^{-2} yr^{-1}

3) Energy in kinetic energy of rain of direct catchment

Average rainfall at Bromley Works = 553 mm (Knox & Kilner, 1973)
Area of estuary = 6×10^6 m^2

Raindrop size is related to fall velocity and kinetic energy as follows (H.T. Odum *et al.*, 1978)

drop diameter (mm)	fall velocity (cm sec^{-1})	kinetic energy (10^{-6} kcal cm^{-3})
1.0	427	2.17
2.0	579	4.00
3.0	701	5.85
4.0	762	6.91
5.0	792	7.47

Kinetic energy (KE) = [annual rainfall] [KE energy value of drops] assuming a drop size of 4.0 mm

$$KE = (55.3 \text{ cm})\ (100^2 \text{ cm}^2 \text{ m}^{-2})\ (6.91 \times 10^{-6} \text{ kcal cm}^{-3})\ (4.187 \text{ kJ kcal}^{-1})$$

$$= 16.0 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

Quality factor = 2.38×10^5 (H.T. Odum *et al.*, 1978)

Solar equivalents = $3.81 \times 10^6 \text{ kJ}_{SE} \text{ m}^{-2} \text{ yr}^{-1}$

4) Rain gravitational potential energy

Assuming: average annual rainfall = 55.3 cm
mean difference in elevation = 1.0 m

∴ (from H.T. Odum *et al.*, 1978: 37)

$$P.E. \simeq 2 \text{ kcal m}^{-2} \text{ yr}^{-1}$$
$$\simeq 8.4 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

Quality factor = 4.0×10^3 (H.T. Odum *et al.*, 1978)

Solar equivalents = $3.36 \times 10^4 \text{ kJ}_{SE} \text{ m}^{-2} \text{ yr}^{-1}$

5) Chemical free energy of water mixing

The basic equation for the free energy in a chemical gradient is

$$\Delta F = F_0 + nRT \ln (C_1/C_2)$$

where ΔF = the chemical potential energy due to differences in water parity

ΔF_0 = free energy at standard state

n = moles of solids at concentration C_1

R = universal gas constant (1.99 cal/mole °K)

T = temperature (°K)

C_2 = concentration of solute in sea water

C_1 = concentration of solute in inflowing water

(H.T. Odum *et al.*, 1978; Jansson & Zucchetto, 1978)

5A) Direct catchment rainwater

$C_1 = 5$ (H.T. Odum *et al.*, 1978)
$C_2 = 33\,000$ (Knox & Kilner, 1973)

Rainfall = 55.3 cm yr^{-1} (Knox & Kilner, 1973)
Area of estuary = $6 \times 10^6 \text{ m}^2$ (Macpherson, 1978)

$\Delta F = 0 + (1/35)\ (1.99)\ (300)\ \ln (5/33\,000) = -150 \text{ cal g}^{-1}$ solute

at 33 g solute l^{-1} = 4950 cal l^{-1} = 20.7 kJ l^{-1}

rain vol = $3.3 \times 10^6 \text{ m}^3 \text{ yr}^{-1} = 3.3 \times 10^9 \text{ l yr}^{-1}$

total free energy of mixing = $4.95 \times 3.32 \times 10^9 = 1.6 \times 10^{10} \text{ kJ yr}^{-1}$

or $2.7 \times 10^3 \text{ kJ m}^{-2} \text{ yr}^{-1}$

5B) River discharge

$C_1 \simeq 100$ ppm
$C_2 = 33\,000$
annual river discharge (Avon & Heathcoate) $= 1.4 \times 10^8$ m^3 yr^{-1}

$\Delta F = 0 + (1/35)\ (1.99)\ (300)\ \ln\ (100/33\,000) = -99$ cal g^{-1} solute

at 33 g solute l^{-1} = 3263 cal l^{-1} = 13.7 kJ l^{-1}

$\times\ 1.4 \times 10^{11}$ l yr^{-1} $= 1.9 \times 10^{12}$ kJ yr^{-1}

$\div\ 6 \times 10^6 = 3.19 \times 10^5$ kJ m^{-2} yr^{-1}

5C) Oxidation pond discharge

C_1 100 ppm
$C_2 = 33\,000$
annual discharge $= 4.1 \times 10^7$ m^3 yr^{-1} $= 4.1 \times 10^{10}$ l yr^{-1}

$\Delta F = 17.05 \ln (100/33\,000) = -99$ cal g^{-1} solute

at 33 g solute l^{-1} = 13.7 kJ l^{-1}

$\times\ 4.1 \times 10^{10}$ l yr^{-1} $= 5.6 \times 10^{11}$ kJ yr^{-1}

$\div\ 6 \times 10^6 = 9.4 \times 10^4$ kJ m^{-2} yr^{-1}

Quality factor $= 6.9 \times 10^3$ (H.T. Odum *et al.*, 1978)

therefore Solar equivalents

direct catchment rainwater	=	1.9×10^7
river discharge	=	2.2×10^9
oxidation pond discharge	=	6.5×10^8

6) Nutrient chemical potential (H.T. Odum *et al.*, 1978)

Basic equations for nitrogen and phosphorus:

$\Delta F = nRT\ [J_1\ C_1\ \ln\ (C_1/C_2)]$

where J_1 = any annual rainwater input (m^3 yr^{-1})

C_1 = any nutrient content of that water

C_2 = average nutrient content of seawater.

6A) Rainfall (direct catchment)

Assume n = 1/40 for nitrogen
1/95 for phosphorus

C_2 nitrogen = 0.5

C_2 phosphorus = 0.07

C_1 nitrogen = 0.2

C_2 phosphorus = 0.15

$J_1 = .553$ m yr^{-1} $\times\ 6 \times 10^6$ m^2 $= 3.3 \times 10^6$ m^3

T = 300°

6A) Cont'd

$$\Delta F_{nitrogen} = \frac{1.99 \times 10^{-3} \text{ kcal mole } °K \times 300°K}{40 \text{ g mole}} \left[(3.3 \times 10^6)\ (.2)\ \ln\left(\frac{.2}{.5}\right)\right]$$

$$= 1.5 \times 10^{-2} \times 6.0 \times 10^5$$

$$= 9.07 \times 10^3 \text{ kcal yr}^{-1} \ (\times 4.187 \text{ kJ kcal}^{-1})$$

$$= 3.8 \times 10^4 \text{ kJ yr}^{-1} \ (\div 6 \times 10^6 \text{ m}^2)$$

$$= 6.3 \times 10^{-3} \text{ kJ m}^{-2} \text{ yr}^{-1}$$

Quality factor = 5.8×10^8

∴ Solar equivalents = $3.7 \times 10^6 \text{ kJ}_{SE} \text{ m}^{-2} \text{ yr}^{-1}$

$$\Delta F_{phosphorus} = \frac{1.99 \times 10^{-3} \times 300}{95} \left[(3.3 \times 10^6)\ (.15)\ \ln\left(\frac{.15}{.07}\right)\right]$$

$$= 6.3 \times 10^{-3} \times 3.77 \times 10^5$$

$$= 2.4 \times 10^3 \text{ kcal yr}^{-1}$$

$$= 1.6 \times 10^{-3} \text{ kJ m}^{-2} \text{ yr}^{-1}$$

Quality factor = 5.2×10^9

∴ Solar equivalents = 8.6×10^6

6B) River discharge

	Avon R.	Heathcote R.	Notes
flow (m^3 yr^{-1})	1.0×10^8	3.5×10^7	Knox & Kilner, 1973
nutrient conc. (g m^{-3})			
Total N	1.13	4.09	Knox & Kilner, 1973
Total P	0.075	0.06	Robb, 1973

$$\Delta F_{nitrogen\ Avon} = \frac{1.99 \times 10^{-3} \times 300}{40} \left[(1.0 \times 10^8)(1.13)\ \ln\left(\frac{1.13}{.5}\right)\right]$$

$$= (1.5 \times 10^{-2}) \quad (9.2 \times 10^7)$$

$$= 1.4 \times 10^6 \text{ kcal yr}^{-1}$$

$$= .96 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

$$\text{Heathcote} = (1.5 \times 10^{-2}) \left[(3.5 \times 10^7)(1.13)\ \ln\left(\frac{1.13}{.5}\right)\right]$$

$$= 4.8 \times 10^5 \text{ kcal yr}^{-1}$$

$$= .34 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

$\Delta F_{nitrogen}$ total for river inflow

$$= 1.30 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

Quality factor = 5.8×10^8

therefore Solar equivalents = $7.5 \times 10^8 \text{ kJ}_{SE} \text{ m}^{-2} \text{ yr}^{-1}$

$\Delta F_{phosphorus}$

Avon $= \frac{1.99 \times 10^{-3} \times 300}{95} [(1.0 \times 10^{8})(0.075) \ln (\frac{0.075}{0.07})]$

$= 3.3 \times 10^{3}$ kcal yr^{-1}

$= 2.2 \times 10^{-3}$ kJ m^{-2} yr^{-1}

Heathcote $= \frac{1.99 \times 10^{-3} \times 300}{95} [(3.5 \times 10^{7})(0.06) \ln (\frac{0.06}{0.07})]$

$= 2.039 \times 10^{3}$ kcal yr^{-1}

$= 1.4 \times 10^{-3}$ kJ m^{-2} yr^{-1}

Total river $\Delta F_{nitrogen}$ $= 3.6 \times 10^{-3}$ kJ m^{-2} yr^{-1}

Quality factor $= 5.2 \times 10^{9}$

$\therefore$ Solar equivalents $= 1.9 \times 10^{7}$ kJ_{SE} m^{-2} yr^{-1}

6C) Oxidation pond discharge

Annual flow $= 4.1 \times 10^{7}$ m^{3} yr^{-1} (Knox & Kilner, 1973)

Mean total N $= 25.46$ g m^{-3} (Knox & Kilner, 1973)

Mean total P $= 3.79$ g m^{-3} (Robb, 1973)

$\Delta F_{nitrogen} = \frac{1.99 \times 10^{-3} \times 300}{40} [(4.1 \times 10^{7})(25.46) \ln (\frac{25.46}{.5})]$

$= 6.2 \times 10^{7}$ kcal yr^{-1}

$= 42.9$ kJ m^{-2} yr^{-1}

Quality factor $= 5.8 \times 10^{8}$

Solar equivalents $= 2.5 \times 10^{10}$ kJ_{SE} m^{-2} yr^{-1}

$\Delta F_{phosphorus} = \frac{1.99 \times 10^{-3} \times 300}{95} [(4.1 \times 10^{7})(3.79) \ln (\frac{3.79}{.07})]$

$= 3.9 \times 10^{6}$ kcal yr^{-1}

$= 2.7$ kJ m^{-2} yr^{-1}

Quality factor $= 5.2 \times 10^{9}$

Solar equivalents $= 1.4 \times 10^{10}$ kJ_{SE} m^{-2} yr^{-1}

7) Physical energy in tidal absorption

Tidal energy $E = 1/8\ \rho g H^{2}$ (Ippen, 1966; H.T. Odum *et al.*, 1978)

where ρ = density of seawater = 1.025 g cm^{-3}

g = acceleration due to gravity = 980 cm sec^{-2}

H = mean tidal range (cm) = 80 cm

$$E = 1/8\ (1.025)\ (980)\ (80)^2$$
$$= 8.0 \times 10^5 \text{ erg cm}^2\ (100^2 \text{ cm}^2 \text{ m}^{-2})$$
$$= 8.0 \times 10^9 \text{ erg m}^{-2}$$
$$= 0.8 \text{ kJ m}^{-2}$$

The flux of tidal energy or power to the estuarine system is given as

Tidal power $P = E \sqrt{gh}\ b$

where h = average depth of estuary
b = average width of estuary

therefore

$$P = (0.8 \text{ kJ m}^{-2})\ \sqrt{(9.8 \text{ m sec}^{-2})\ (.8 \text{ m})}$$
$$= 2.24 \text{ kJ sec}^{-1}\ (3.15 \times 10^7 \text{ sec yr}^{-1})$$
$$= 7 \times 10^7 \text{ kJ/m/yr/tide (730 tides yr}^{-1})$$
$$= 5.1 \times 10^{10} \text{ kJ m}^{-1} \text{ yr}^{-1}$$

Assuming an approximate mean estuary width of 500 m

$$P = (5.1 \times 10^{10})\ (500 \text{ m}) = 2.56 \times 10^{13} \text{ kJ yr}^{-1}$$
$$\div\ 6 \times 10^6 \text{ m}^2 = 4.26 \times 10^6 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

Quality factor of tidal energy = 3400 (H.T. Odum *et al.*, 1978)

therefore Solar equivalents

$$= (4.26 \times 10^6)\ (3.4 \times 10^3) = 1.4 \times 10^{10} \text{ kJ}_{SE} \text{ m}^{-2} \text{ yr}^{-1}$$

8A) Physical potential energy in river discharge

river discharge (Avon & Heathcote) = $1.4 \times 10^8 \text{ m}^{-3} \text{ yr}^{-1}$

mean elevation ≃ 5 m.

$$PE = (1 \text{ g cm}^{-3})(1.4 \times 10^8 \text{ m}^3 \text{ yr}^{-1})(10^6 \text{ cm}^3 \text{ m}^{-3})(980 \text{ cm sec}^{-1})$$
$$(500 \text{ cm})\ (10^{-10} \text{ kJ erg}^{-1})$$
$$= 6.9 \times 10^9 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

Quality factor = 3.7×10^4

Solar equivalent = $2.6 \times 10^{14} \text{ kJ}_{SE} \text{ m}^{-2} \text{ yr}^{-1}$

8B) Physical potential energy in oxidation pond discharge

PE = (mass) (height) (gravity)

$$= (1 \text{ g cm}^{-3})(4.1 \times 10^7 \text{ m}^3 \text{ yr}^{-1})(10^6 \text{ cm}^3 \text{ m}^{-3})(980 \text{ cm sec}^{-1})$$
$$(300 \text{ cm})\ (10^{-10} \text{ kJ erg}^{-1})$$
$$= 1.2 \times 10^9 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

Quality factor = 3.7×10^4 (H.T. Odum *et al.*, 1978)

Solar equivalent = $4.4 \times 10^{13} \text{ kJ}_{SE} \text{ m}^{-2} \text{ yr}^{-1}$

9) Energy in waves breaking (H.T. Odum *et al.*, 1978; Ippen, 1966)

Wave energy = $E = 1/8\ pg\ H^2$

where p = density of sea water = $1.025\ g\ cm^{-3}$

g = acceleration of gravity = $980\ cm\ sec^{-2}$

H = mean wave height.

Mean wave height = .2 m (Macpherson, 1978)

$$E = 1/8\ (1.025\ g\ cm^{-3})\ (980\ cm\ sec^{-2})(20\ cm)^2\ (100^2\ cm^2\ m^{-2})\ (10^{-10}\ ergs\ kJ^{-1}).$$

$$= 5 \times 10^{-2}\ kJ\ m^{-2}$$

Wave power = $P = EC$

where C = wave celerity

$= \sqrt{gd}$ for shallow water

d = mean water depth

$$P = E\sqrt{gd}$$

$$= E\sqrt{9.8(d)}\ (3.15 \times 10^7\ sec\ yr^{-1})\ (4.187\ kcal\ kJ^{-1})$$

$$= 4.1 \times 10^8\ E\sqrt{d}\ kJ\ m^{-1}\ yr^{-1}$$

$$= (4.1 \times 10^8)\ (5 \times 10^{-2})\ (\sqrt{.8})$$

$$= 1.8 \times 10^7\ kJ\ m^{-1}\ yr^{-1}$$

for any wind direction, the maximum exposed length of shoreline is approximately 1000 m

$\therefore$ wave power = $P \times 1000 = 1.8 \times 10^{10}\ kJ\ yr^{-1}$

on an areal basis

$\div\ 6 \times 10^6 = 3.1 \times 10^3\ kJ\ m^{-2}\ yr^{-1}$

Quality factor = 5.09×10^4 (H.T. Odum *et al.*, 1978)

Solar equivalent = $1.6 \times 10^8\ kJ_{SE}\ m^{-2}\ yr^{-1}$

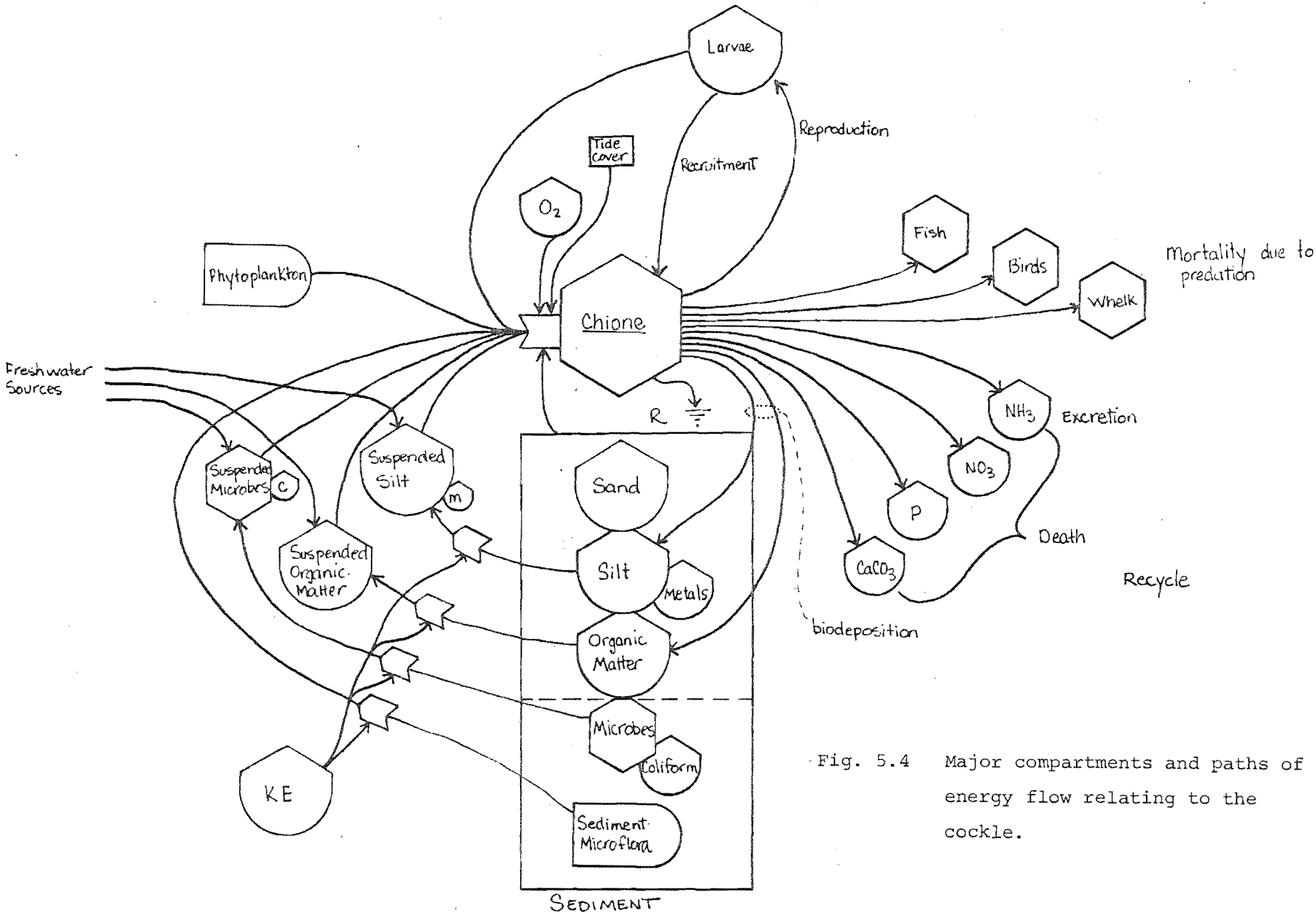


Fig. 5.4 Major compartments and paths of energy flow relating to the cockle.

matter to benthic decomposers (as faeces and pseudofaeces), predators (especially oystercatchers, fish, and whelks) and inorganic matter to the sediments for slow recycle upon death.

Two sub-models involving *C. stutchburyi* were investigated from the web of energy flow in the Avon-Heathcote Estuary (Fig. 5.3). In each case, symbolic energy language modules (Fig. 5.1) were used to show the major pathways, flows and variables as well as interactions. From the flow diagram, the system was described in a series of inherent, simultaneous, non-linear differential equations and simulated (in extended BASIC) on a micro computer (Compucolor II).

5.2.1 Daily Model

This model (Fig. 5.5) links the flow of energy through the cockle and oystercatcher populations on a time scale of hours, and was used to investigate the relationship between observed behavioural aspects of the predators and energy flow. The aims were to calculate the energy flux along this path; and to estimate the effect of this predator on the cockle population, and ultimately on the estuary.

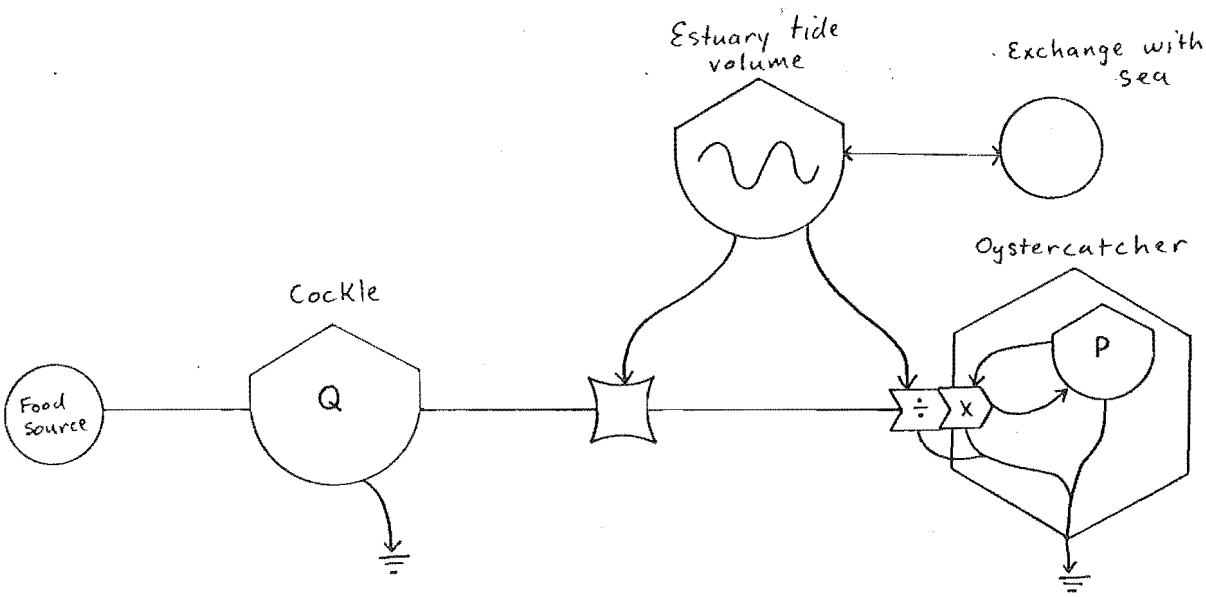


Fig. 5.5 Daily model of energy flow through the cockle and oystercatcher compartments of the Avon-Heathcote Estuary.

Data for the oystercatcher population dynamics and behaviour are from Baker (1966, 1969, 1972, 1973) and Knox & Kilner (1973).

In the model, a food source (suspended organic matter and phytoplankton) is utilised by *C. stutchburyi* (here represented as a simple tank) which in turn is fed upon by the oystercatcher.

Baker (1969) has shown that oystercatchers feed according to the tidal cycle, with maximum numbers at low tide. These birds feed at the water line, and as cockles are limited to the lower part of the shore, oystercatcher feeding is limited to the time during which the tide is below 1.4 m (where 0 = extreme low tide). This is represented in the model by a switch (K4). The tide is represented by a sine curve.

Estimated initial values (weights) were placed on the diagram of the model (Fig. 5.6) and used to calculate constants for the differential equations (Table 5.2).

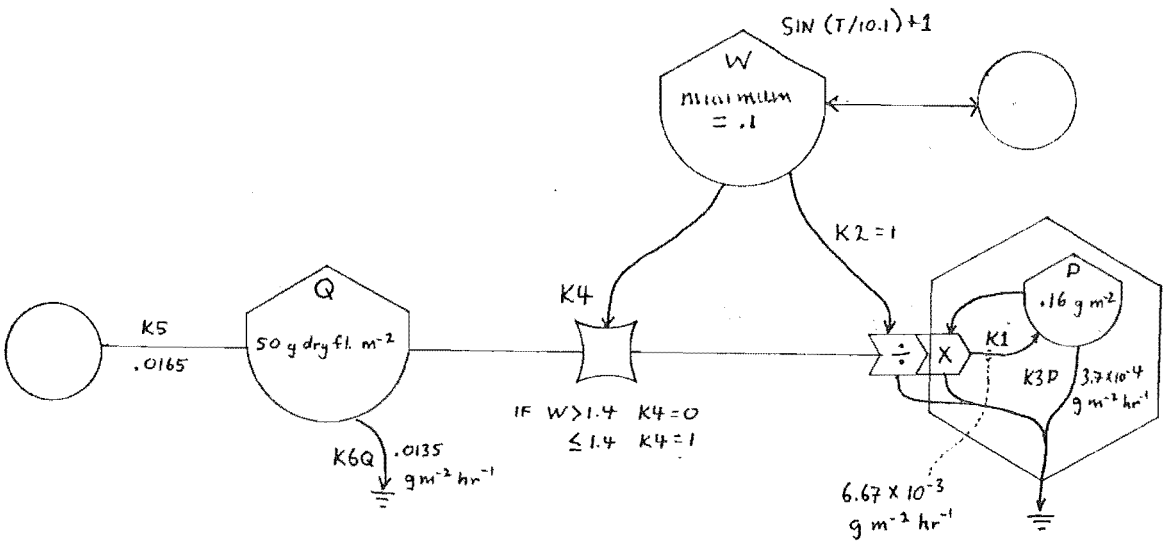


Fig. 5.6 Daily model of energy flow through cockles and oystercatchers, with rates of transfer of matter between the compartments.

The model (listed as Table 5.3) caused oscillations in both cockle and oystercatcher biomass in response to the forcing function of tide cycle. The results after five complete tides are shown in Table 5.4.

Table 5.2 Constants for the daily energy flow model of cockles and oystercatchers in the Avon-Heathcote Estuary.

Path	Eqn	Constant	Value
Cockle respiration	K6Q = .0135	K6 = .0135/50	K6 = 2.7 E - 4
Cockle assimilation	K5	set at	K5 = .0165
Switch	K4	If W>1.4 then If W<1.4 then	K4 = 0 K4 = 1
Oystercatcher metabolism	$K3P = 3.7 \times 10^{-4}$	K3 = .00037/.16	K3 = 2.3 E - 3
Tide	K2W	= tide vol. eqn	K2 = 1
Oystercatcher feeding	K1*K4*P*Q*(1/(K2*W)) $= 6.67 \times 10^{-3}/(1)(.16)(50)(10)$		K1 = 8.3 E - 5

As initially set up, *C. stutchburyi* biomass remained stable, but oystercatcher biomass increased rapidly. Manipulation of oystercatcher metabolism (K3) led to stability in the model.

Table 5.3 Program list for daily model of energy flow through cockles and oystercatchers.

```
10  K1=8.3 E-5
20  K2=1
30  K3=2.3 E-3
40  K4=1
50  K5-.0165
55  K6=2.7 E-4
60  T=0
80  Q=50
90  P=.16
100 W=(SIN(T/10.1))+1
105 IF W<.1 THEN W=.1
110 IF W>1.4 THEN K4=0
120 IF W<1.4 THEN K4=1
121 IF W=1.4 THEN K4=1
130 Q=Q+K5-K6*Q-K4*K1*P*Q*(1/(K2*W))
140 P=P+K1*P+Q/W*K4-K3*P
```

.../Cont'd

Table 5.3 - Cont'd

```
160 PLOT 2,T,(10*W)+20,255
170 PLOT 29,17
180 PLOT 2,T,(Q-49)*50,255
190 PLOT 29,18
200 PLOT 2,T,(50*P)+70,255
202 PLOT 29,19
204 PLOT 2,T,(5*K4)+100,255
210 T=T+1
220 IF T<127 THEN 100
230 PRINT (T/5.29)
240 PRINT P
250 PRINT Q
260 END
```

Table 5.4 Values generated by daily submodel of the Avon-Heathcote Estuary.

As stored

after 5 tides (127 hrs) *Chione* biomass Q = 50

Oystercatcher P = .45

	Q	P
1) Varying K5 (*Chione* assimilation)		
after 127 hrs		
K5 = .01	49.2	.4437
K5 = .0165	50.01	.4485
K5 = .02	50.44	.451
K5 = .04	52.92	.467
2) Varying K1 (feeding rate)		
$K1 = 4 \times 10^{-5}$	50.2	.227
$K1 = 8.3 \times 10^{-5}$	50.01	.4485
$K1 = 10 \times 10^{-5}$	49.9	.59
3) Varying K3 (oystercatcher metabolism)		
$K3 = 2.3 \times 10^{-3}$	50.01	.4485
$K3 = 4.6 \times 10^{-3}$	50.06	.336
$K3 = 8 \times 10^{-3}$	50.1	.21
$K3 = 10 \times 10^{-3}$	50.16	.169

5.2.2 Yearly Model

A second model, with a daily time increment, was aimed at stimulating yearly energy flow through the major paths involving *C. stutchburyi* (Fig. 5.7). Forcing functions include nutrients and organic matter from the rivers, oxidation ponds and sea, temperature and sunlight. Major compartments are cockles, oystercatchers, suspended organic matter, detritus, algae and an estuarine nutrient pool. Paths are shown in Fig. 5.8, and flows calculated as shown in Tables 5.5 to 5.10.

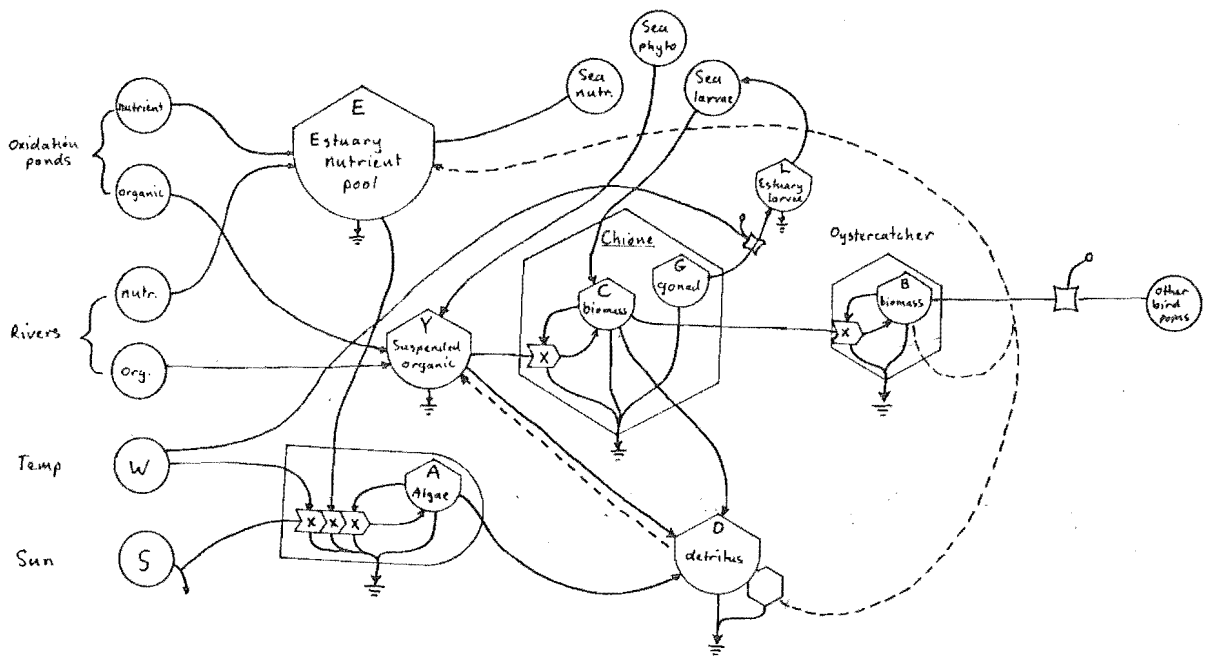


Fig. 5.7 Yearly model of energy flow through *C. stutchburyi* and related compartments of the Avon-Heathcote Estuary.

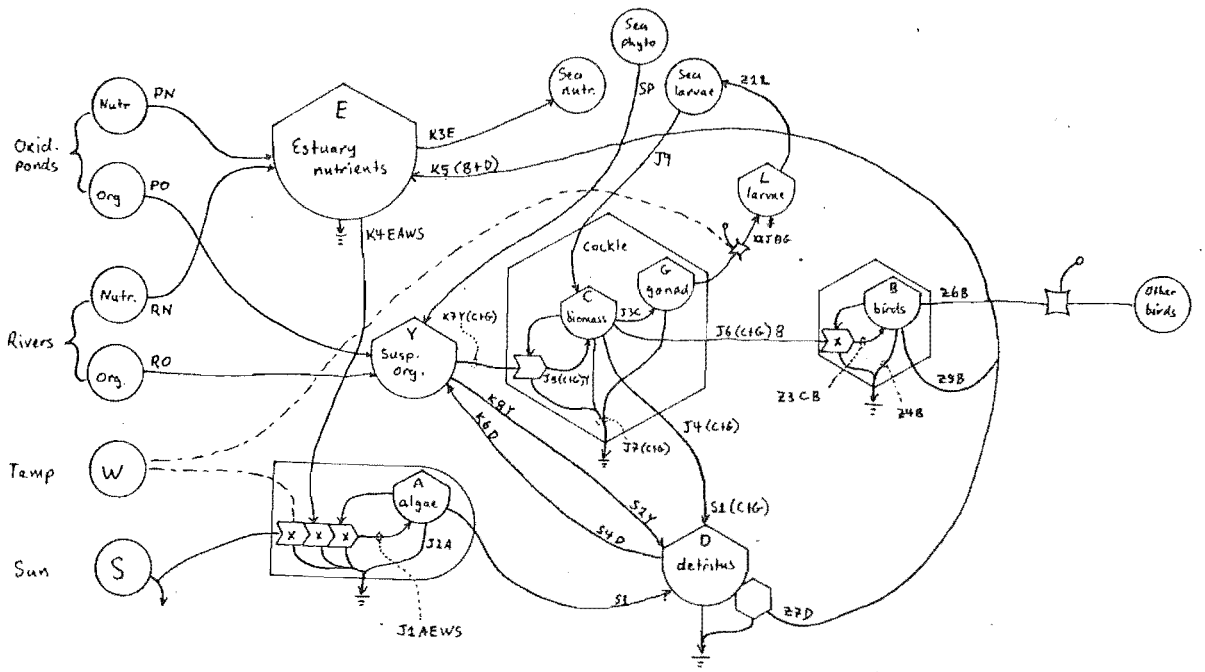


Fig. 5.8 Compartments and energy flow pathways in the yearly submodel of the Avon-Heathcote Estuary.

Table 5.5 Calculation of constants for the yearly model of the Avon-Heathcote Estuary; Fig. 5.8.

S = Solar input - recorded values for A.H.E. (Knox & Kilner, 1973)

Winter input = 1000 Kcal m^{-2} dy^{-1}
Summer input = 6000 Kcal m^{-2} dy^{-1}

therefore S = (cos(T/58.12) + 1) * 2500 + 1000, starting in mid January.

W = Temperature - data from Knox & Kilner (1973)

Maximum water temperature = 22°C, mid January.
Minimum water temperature = 8°C, mid July.

∴ W = (cos(T/58.12) + 1) * 7 + 8, starting in mid January.

PN = Nutrient input from oxidation ponds. Sum of nitrogen + phosphorus. Data from Robb (1974), Knox & Kilner (1973). See calculations in Table 5.1.

PN = .479 gN m^{-2} dy^{-1} + .071 gP m^{-2} dy^{-1} = .55 g m^{-2} dy^{-1}

RN = Nutrient input (nitrogen + phosphorus) from the Avon and Heathcote Rivers. See PN calculation.

RN = .119 gN m^{-2} dy^{-1} + .043 gP m^{-2} dy^{-1} = .16 g m^{-2} dy^{-1}

PO = Organic input from oxidation ponds.

Set at .5 g m^{-2} dy^{-1}

RO = Organic matter in river flow.

Set at .2 g m^{-2} dy^{-1}

SP = Phytoplankton from the sea.

Set at .2 g m^{-2} dy^{-1}

B = Oystercatcher biomass. Observations of oystercatcher populations on the Avon-Heathcote Estuary (Sagar, pers. comm. and Baker, 1973) reveal a seasonal pattern to oystercatcher numbers. (See further calculations in Tables 5.6 and 5.7.)

B winter - January 15 for 215 days

Mean popn = 2600 birds, mean wet wt = 494 g
Assume dry wt = 33.7% of wet.
= 4.3×10^5 g dry wt
÷ 6×10^6 m^2 area = .072 g dry m^{-2}

B summer - (days 216 - 365)

Mean popn = 550 birds, mean wet wt = 494 g
Assume dry wt = 33.7% of wet
= 9.2×10^4 g dry wt
÷ 6×10^6 m^2 area = .015 g dry m^{-2}

K3E - nutrient loss to sea. 56% loss during each of two tides per day.

K3 = .87

K4 EA - nutrient loss to algae. Nutrients set down in 10:1 ratio of N:P in algae and a mean total of approximately 3% of algae dry biomass (Knox & Kilner, 1973).

When algal accumulation rate = 6 g m^{-2} dy^{-1}, then K4 EAWS = .018.

Therefore $K4 = \frac{.018}{.3\times100\times6000\times22} = 4.55\ E\text{-}9$

K5 (B+D) = nutrients from recycle
K5(B+D) estimated to be 0.045 g m^{-2} dy^{-1}

$\therefore$ K5 = .045/(30 + .072) = 1.5 E-3

J1 AEWS = Algae accumulation rate (see Fig. 5.10).

= 6 gC m^{-2} dy^{-1}

$J1 = \frac{6}{100\times.3\times6000\times22} = 1.5\times10^{-6}$

J2 A = Algal respiration.

J2 estimated to be 0.007.

K7 Y(C+G) - loss of suspended organic matter to *Chione*

Feeding rate of *Chione* (Table 5.8)
= 6 g m^{-2} dy^{-1}

K7 Y(C+G) = 6; $K7 = \frac{6}{10(25+12)} = .0162$

J5 (C+G)Y - feeding of *Chione* (Table 5.8) = 6.

J5 = .0162

J7 (C+G) - *Chione* respiration (Table 5.8)

J7 = .05

J3 C - *Chione* gonad accumulation over 90 days (260-350)

= 12/90 = .133 g m^2 dy

$J3 = \frac{.133}{24} = .0056$ (0 to start).

J6 (C+G)B - loss of *Chione* to oystercatchers (Table 5.7)

Winter = 4.17×10^{-2}; $J6 = \frac{4.7 \times 10^{-2}}{37 \times .072} = .018$

Z3 (C+G)B - ingestion by oystercatchers (Table 5.7)

Winter; Z3 = .018

Z4 B - oystercatcher respiration (Table 5.7)

Winter = 2.29×10^{-2}; $Z4 = \frac{.0229}{.072} = .318$

Z5 B - oystercatcher recycle (Table 5.7)

Winter = 1.25×10^{-2}; $Z5 = \frac{1.25 \times 10^{-2}}{.072} = .174$

Summer oystercatcher values (Table 5.7)

Z3 = .0083/(C+G).015 Z4 = .32 Z5 = .167

Calculation of Oystercatcher Parameters

The South Island Pied Oystercatcher (*Haematopus ostralegus finschi*) is represented in the model as shown in Fig. 5.9

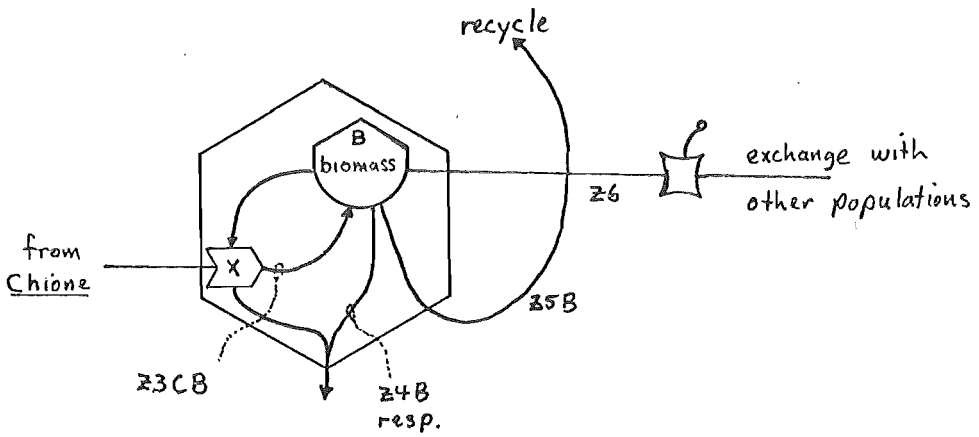


Fig. 5.9 Module representing dynamics of the oystercatcher in the Avon-Heathcote Estuary.

The number of oystercatchers at the Avon-Heathcote Estuary varies seasonally, as the majority of the flock migrate between breeding grounds (probably inland Canterbury) and the estuary. Results of monthly counts made in 1977 (P. Sagar, pers. comm.) are shown in Table 5.6.

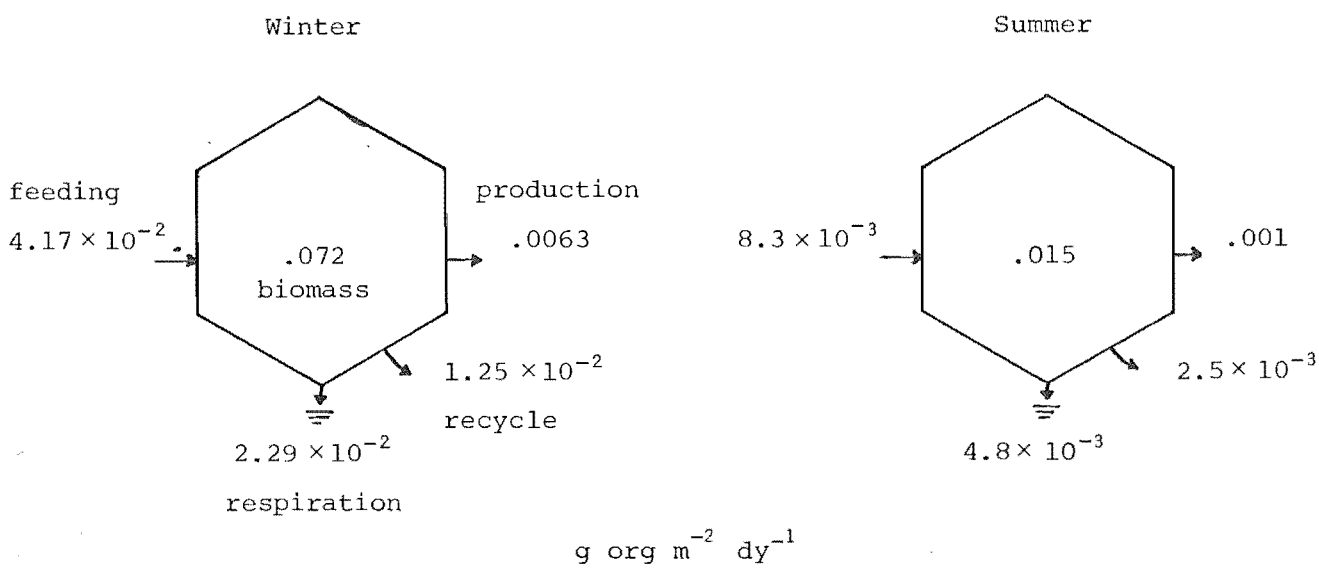
Table 5.6 Counts of the South Island Pied Oystercatcher in the Avon-Heathcote Estuary during 1977. (P. Sagar, pers. comm.)

Date	Number	Date	Number
17/10/76	438	25/ 6/77	2720
20/11/76	402	23/ 7/77	2206
18/12/76	537	4/ 9/77	679
15/ 1/77	1356	23/10/77	652
26/ 2/77	3710	4/12/77	528
26/ 3/77	2387	20/12/77	630
30/ 4/77	2865	20/ 1/78	3420
28/ 5/77	2400		

For the purpose of the model, the oystercatcher population was considered in two distinct subunits; a winter phase (from January 15, for 215 days) and a summer phase (days 216 to 365). Initial oystercatcher parameters were set (on day 1 and day 216) each year as calculated in Table 5.7.

Table 5.7 Calculation of "winter" and "summer" parameters for the oystercatcher population of the Avon-Heathcote Estuary.

	Winter	Summer
Months	mid Jan - mid Aug	mid Aug - mid Jan
Time	215 days	150 days
Model days	1 - 215	216 - 365
Mean population density	2600	550
Total oystercatcher biomass $(wet)_A$	1.3×10^6 g	2.7×10^5 g
Total biomass $(dry)_B$	4.3×10^5 g	9.2×10^4 g
Biomass per square metre $_C$	.072 g dry m^{-2}	0.15 g dry m^{-2}
Respiration $_D$ g dry m^{-2} dy^{-1}	2.29×10^{-2}	4.8×10^{-3}
Consumption $_E$ g dry org m^{-2} dy^{-1}	4.17×10^{-2}	$8.3 \quad 10^{-3}$
Assimilation $_F$ g dry org m^{-2} dy^{-1}	2.9×10^{-2}	5.8×10^{-3}
Excretion $_G$ g dry org m^{-2} dy^{-1}	1.25×10^{-2}	2.5×10^{-3}



Footnotes to Table 5.7:

A mean oystercatcher live weight = 494 g (Baker, 1969)

B assuming dry wt = 33.7% of wet wt

C AHE mudflat area = 6×10^6 m^2

D Respiration assumed to be 32% body weight per day (Altman & Dittmer, 1971; Prosser & Brown, 1961)

E Consumption:

	Winter	Summer
Feeding rate (Baker, 1969) *Chione* hr^{-1} $bird^{-1}$ =	34.25	32.5
Assuming 12 hrs feeding per day *Chione* dy^{-1} $bird^{-1}$ =	411	390
Assuming mean *Chione* length of 25 mm ln wt = -10.4 + 2.78 ln length (section 2) = .234 g ash-free dry wt ind^{-1}		
∴ AFDW *Chione* consumed dy^{-1} $bird^{-1}$ =	96.3	91.3
At popn levels stated g AFDW *Chione* consumed dy^{-1} =	2.5×10^5	5.02×10^4
At 6×10^6 m^2 area g AFDW *Chione* consumed m^{-2} dy^{-1} =	4.17×10^{-2}	8.3×10^{-3}

F Assimilation: assuming an assimilation efficiency of 70% (Browder, 1978 used 79%)

from E;		
g AFDW *Chione* assim. $bird^{-1}$ dy^{-1}	67.4	63.9
total g AFDW *Chione* assim. dy^{-1}	1.75×10^5	3.5×10^4
g AFDW *Chione* assim. m^{-2} dy^{-1}	2.9×10^{-2}	5.8×10^{-3}

G Excretion; FU = C-A, therefore excretion = 30%

from E + F		
g AFDW *Chione* excr $bird^{-1}$ dy^{-1}	28.9	27.4
total g AFDW *Chione* excr dy^{-1}	7.5×10^4	1.5×10^4
g AFDW *Chione* excr m^{-2} dy^{-1}	1.25×10^{-2}	2.5×10^{-3}

Calculation of algal parameters

Two green algae, *Ulva lactuca* L. and *Enteromorpha ramulosa* are abundant in the Avon-Heathcote Estuary, and they are represented in the model as in Fig. 5.10

Green algae increased in density from 1946 (Wilkinson, 1963) until at least 1973 (Knox & Kilner, 1973), although this trend appears to have been reversed in recent years (see section 2). Algal biomass varies seasonally, with a peak in the summer (Steffensen, 1974; Knox & Kilner,

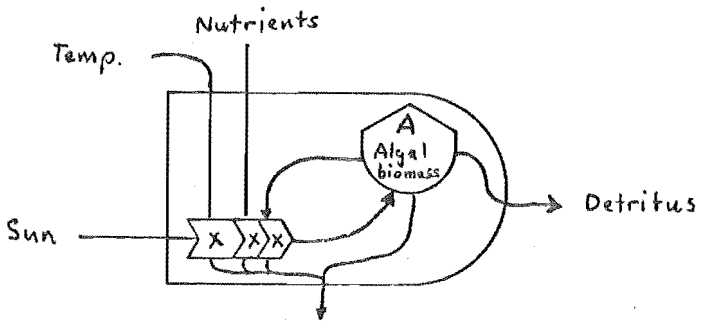


Fig. 5.10 Algal module of the Avon-Heathcote Estuary yearly model.

1973). Using records of algal cover and biomass (Knox & Kilner, 1973) and assuming that dry weight is 10% of wet weight; seasonal biomass was calculated (from the year 1969/70) to be 125 g dry wt m^{-2} in January, 75 g m^{-2} in April and 50 g m^{-2} in July and October. Waite & Mitchell (1972) estimated net production of *Ulva* to be 2 - 8 mgC g(dry wt)$^{-1}$ hr^{-1} and demonstrated the effect of N and P levels on production. Laboratory experiments (Steffensen, 1974) show that N and P levels of the Avon-Heathcote Estuary are below optimal for maximal *Ulva* production.

Assuming a net production of 5 mgC g(dry algae)$^{-1}$ dy^{-1} and 12 hours of production per day, total algal production = 6 g C m^{-2} dy^{-1}.

Calculation of *C. stutchburyi* parameters

C. stutchburyi is represented in this model as in Fig. 5.11.

Flows and storage values are based on calculations from section 4, and on the daily submodel; applied to a theoretical population with a summer biomass of 33 g and gonad of 12 g (ash-free dry wt m^{-2}). Constants are calculated in Table 5.8.

Operation of the model

The model is listed in Table 5.9. With an optional statement (line 819) the program gives printed values; without it the values are plotted on a graph.

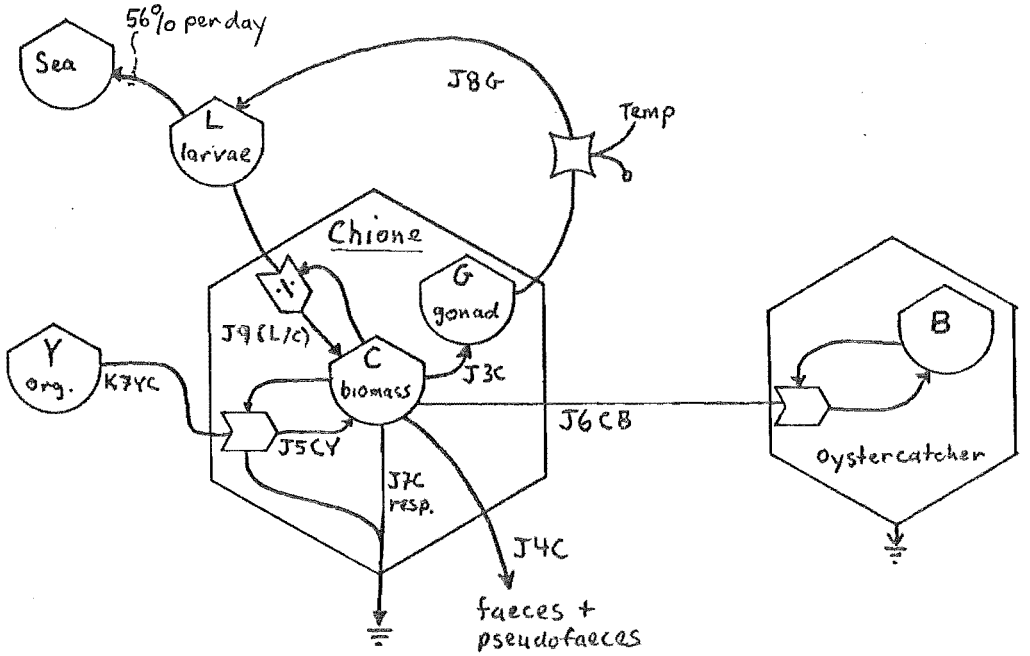
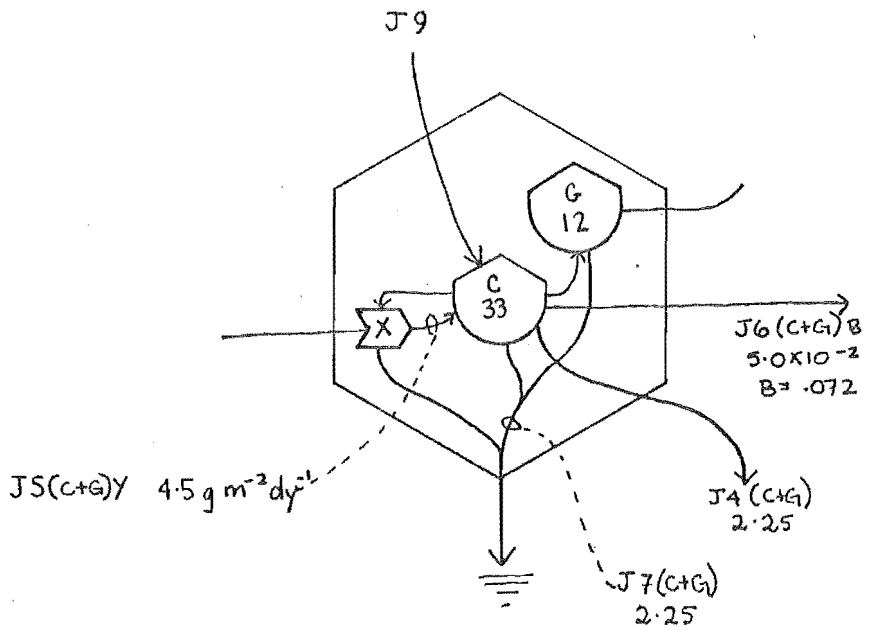


Fig. 5.11 Representation of the cockle module of the yearly Avon-Heathcote Estuary model.

A sample of the values generated by the model are presented in Table 5.10 (years 1, 2, 3 and 10). Seasonal oscillations were present in most parameters in response to the fluctuations in forcing functions (solar radiation and temperature). However, all parameters were stable from year to year, after an initial period of adjustment in the first year. Notably, the value of *Chione* biomass (C) increased from 33 g m^{-2} in the first year to 36 g m^{-2} at the beginning of the second and subsequent years; while *Chione* gonad weight decreased from 12 g m^{-2} to 4.9 g m^{-2} over the same period. Seasonal fluctuations in the data generated by the model were similar to patterns observed in the estuary.

This model allowed investigation of specific alterations to the ecosystem. For example, the effect of increased nutrient and organic input from the Bromley Oxidation Ponds on the algal, detritus, suspended matter, cockle population and oystercatcher population was simulated.

Table 5.8 Calculation of constants for the *Chione* module of the Avon-Heathcote Estuary yearly model (January).



J6 = loss to oystercatchers $J6(C+G)B = 5.0 \times 10^{-2}$

$$J6 = \frac{5.0 \times 10^{-2}}{(C+G)B} = 1.56 \times 10^{-2}$$

J4 = faeces + pseudofaeces at 5% of total weight

$J4(C+G) = 2.25$

$J4 = .05$

J7 = respiration at 5% of body weight per day

$J7(C+G) = 2.25$

$J7 = .05$

J5 = feeding $J5(C+G)Y \simeq 6$ (when Y = 8)

$J5 = .0124$

In the first simulation (Table 5.11) oxidation pond discharge was eliminated from the model from the beginning (T=0). An initial drop in suspended organic matter (Y) during the first 25 days resulted in a drop in *Chione* biomass (C) and oystercatcher biomass (B). Suspended organic matter then peaked at day 75 and reached a stable level (near the original) by day 200. Cockle biomass levelled off at 42% of the original biomass. Oystercatcher biomass decreased greatly under these conditions. Most parameters stabilised after two years, but algal biomass continued to decline.

Table 5.9 Program list for the Avon-Heathcote Estuary yearly model.

```
5 PLOT 2,0,0,242,0,0,0,127,127,127,127,0,0,0,255
7 PPP=1
10 E=.3
20 Y=8
30 A=100
40 C=33
50 G=12
60 L=0
70 D=30
80 B=.072
85 XX=0
86 ZX=0
87 ZZ=100
130 PN=.55
140 PO=.5
150 RN=.16
160 RO=.2
170 SP=.2
220 K3=.87
230 K4=4.5E-9
240 K5=1.5E-3
250 K6=.001
268 K7=.00162
270 K8=.01
280 K9=0
300 J1=1.4E-7
310 J2=.007
320 J3=0
330 J4=.05
340 J5=.0124
350 J6=1.56E-2
360 J7=.05
370 J8=.0056
380 J9=0
400 S1=.1
410 S2=.01
420 S3=0
430 S4=.154
500 Z1=0
510 Z2=.87
520 Z3=.0145
530 Z4=.318
540 Z5=.174
550 Z6=0
560 Z7=.001
600 X=1
610 T=1
615 I=1
619 IF T=350 OOTO 993
620 IF T=216 GOTO 900
621 IF T=365 GOTO 950
630 IF W>21.96 GOTO 980
632 V=V-1
634 IF V=0 GOTO 985
```

Table 5.9 - Cont'd

```
635 IF T=20 GOTO 987
637 IF T=110 GOTO 989
638 W+(COS(T/58.12)+1)*7+8
690 S=(COS(T/58.12)+1+*2500+1000
720 E=E+PN+RN+K5*(B+D)-K3*E-K4*E*A*W*S
721 IF E<0 THEN E=0
730 Y=Y+SP+PO+RO+K6*D-K7*Y*(C+D)-K8*Y
740 A=A+J1*A*E*W*S-J2*A
741 ZX=ZZ-A
742 IF ZX<0 THEN ZX=0
743 ZZ=A
744 S3=ZX
750 C=C+J5*(C+G)*Y+J9-J3*C-J6*(C+G)*B-J4*(C+G)-J7*(C+G)
760 D=D+S1*(C+G)+S2*Y+S3-S4*D-S7*D
765 FF=Z3*C*B
766 IF X<216 GOTO 996
767 IF FF>8.3E-3 THEN FF=8.3E-3
770 B=B+FF-Z4*B-Z5*B-Z6*B
775 G=G+J3*C-XX*J8*G
780 L=L+XX*J8*G-Z2*L
800 T=T+1
810 X=X+1
819 GOTO 1005
820 IF X=3 GOTO 849
821 GOTO 620
849 R=T/3
850 PLOT 29,17
851 PLOT 2,R,W/2+110,255
855 PLOT 29,18
856 PLOT 2,R,S/500+105,255
860 PLOT 29,19
861 PLOT 2,R,E*20+15,255
865 PLOT 29,20
866 PLOT 2,R,Y*10,255
870 PLOT 29,21
871 PLOT 2,R,(A/10)*1.5,255
875 PLOT 29,22
876 PLOT 2,R,C+40,255
880 PLOT 29,23
881 PLOT 2,R,B*100+40,255
885 PLOT 29,17
886 PLOT 2,R,D/4,255
890 PLOT 29,18
891 PLOT 2,R,G+90,255
895 PLOT 29,19
896 PLOT 2,R,L*5+60,255
897 X=1
899 GOTO 619
900 B=.015
905 J3=1.52E-3
910 Z3=.0135
911 Z4=.32
912 Z5=.167
915 J6=Z3
940 GOTO 621
950 IF I=20 GOTO 995
```

Table 5.9 - Cont'd

```
955 B=.072
956 J6=1.56E-2
957 Z3=.0145
958 J3=0
960 T=1
965 X=1
970 I=I+1
975 GOTO 620
980 V=90
981 XX=1
982 J8=G/90
984 GOTO 632
985 XX=0
986 GOTO 635
987 J9=6.6E-14
988 GOTO 637
989 J9=0
990 GOTO 638
993 J3=0
994 GOTO 620
995 END
996 IF FF>.04 THEN FF=.04
997 GOTO 770
1000 PRINT I,T,C,G,B,A,D,Y,E
1001 PRINT
1002 GOTO 897
1005 PPP=PPP+1
1007 IF PPP=2 GOTO 1000
1009 IF PPP=50 GOTO 1000
1011 IF PPP=100 GOTO 1000
1013 IF PPP=150 GOTO 1000
1015 IF PPP=200 GOTO 1000
1017 IF PPP=250 GOTO 1000
1019 IF PPP=300 GOTO 1000
1021 IF PPP=350 GOTO 1000
1023 IF PPP=364 GOTO 1000
1027 IF PPP=216 GOTO 1000
1028 IF PPP=217 GOTO 1000
1029 IF PPP=365 GOTO 1040
1030 GOTO 897
1040 PPP=1
1041 GOTO 897
```

Table 5.10 Values generated by the yearly model of the Avon-Heathcote Estuary. T = time (days); C = *Chione* biomass; G = *Chione* gonad; B = oystercatcher biomass; A = algal biomass; D = detritus; Y = nutrients; E = suspended organic matter.

Year	T	C	G	B	A	D	Y	E
1	2	32.93	12	.071	100.7	29.96	8.03	.776
	50	38.56	.226	.081	137.8	25.59	8.24	.802
	100	38.16	.006	.081	146.4	26.52	8.12	.834
	150	35.95	.006	.081	119.9	28.17	8.12	.858
	200	36.10	.006	.081	89.2	27.52	8.20	.860
	216	36.36	.006	.081	81.4	27.19	8.21	.859
	217	36.36	.061	.015	81.0	27.17	8.21	.858
	250	36.53	1.89	.018	69.6	27.02	8.21	.854
	300	36.74	4.67	.026	67.6	27.21	8.19	.839
	350	35.67	7.43	.029	89.3	28.36	8.16	.817
	364	36.05	5.48	.028	99.6	28.38	8.12	.811
2	2	36.05	4.85	.075	101.2	28.09	8.12	.809
	50	38.04	.597	.082	138.5	25.63	8.22	.802
	100	38.15	.083	.082	147.1	26.57	8.12	.833
	150	35.91	.083	.082	120.5	28.21	8.12	.858
	200	36.05	.083	.082	89.6	27.56	8.20	.860
	216	36.31	.083	.082	81.8	27.23	8.21	.859
	217	36.32	.138	.015	81.3	27.20	8.21	.858
	250	36.50	1.96	.017	69.9	27.06	8.21	.854
	300	36.72	4.75	.025	67.9	27.24	8.19	.839
	350	35.65	7.50	.027	89.7	28.39	8.16	.817
	364	36.03	5.51	.026	100.1	28.40	8.12	.810
3	2	36.03	4.88	.075	101.7	28.12	8.12	.809
	50	38.04	.595	.082	139.1	25.63	8.22	.802
	100	38.15	.082	.082	147.6	26.57	8.12	.833
	150	35.90	.082	.082	120.9	28.22	8.12	.858
	200	36.04	.081	.082	90.0	27.57	8.20	.860
	216	36.31	.082	.082	82.1	27.23	8.21	.859
	217	36.31	.137	.015	81.7	27.21	8.21	.859
	250	36.49	1.96	.017	70.2	27.07	8.21	.854
	300	36.72	4.75	.025	68.2	27.24	8.19	.839
	350	35.65	7.50	.027	90.0	28.39	8.16	.817
	364	36.03	5.51	.026	100.5	28.40	8.12	.810
10	2	36.03	4.88	.075	103.7	28.12	8.12	.808
	50	38.04	.595	.082	141.8	25.63	8.22	.801
	100	38.14	.082	.082	150.4	26.60	8.12	.833
	150	35.85	.082	.082	123.3	28.28	8.12	.858
	200	36.00	.082	.082	91.7	27.61	8.20	.860
	216	36.27	.082	.082	83.7	27.27	8.21	.859
	217	36.27	.137	.015	83.2	27.24	8.21	.858
	250	36.47	1.96	.017	71.6	27.08	8.21	.853
	300	36.73	4.74	.025	69.5	27.24	8.19	.839
	350	35.65	7.50	.027	91.7	28.39	8.16	.816
	364	36.04	5.51	.026	102.2	28.41	8.12	.809

Table 5.11 Simulated removal of oxidation pond discharge from the Avon-Heathcote Estuary model.

Program change:

from	130	PN = .55	to	130	PN = 0
	140	PO = .5		140	PO = 0

Year	T	C	G	B	A	D	Y	E
1	2	32.65	12	.071	99.7	30.2	7.53	.226
	50	9.59	.226	3 E-8	84.0	9.6	8.06	.192
	100	14.66	.006	1.4 E-16	65.3	12.2	8.35	.202
	150	13.48	.006	7.7 E-24	47.7	11.5	7.95	.203
	200	13.98	.006	2 E-31	34.0	11.0	8.17	.203
	250	13.81	.728	8.8 E-8	24.5	10.9	8.15	.202
	300	13.81	1.78	1.5 E-15	18.6	11.2	8.17	.202
	350	13.58	2.82	2.3 E-23	15.3	11.5	8.14	.202
	364	13.76	2.49	1.5 E-25	14.6	11.5	8.12	.202
2	2	13.77	2.36	.051	14.5	11.48	8.11	.202
	100	14.68	.259	5.6 E-16	9.5	10.59	8.07	.202
	200	14.74	.259	7.1 E-30	4.9	10.49	8.07	.202
	300	14.05	2.08	2.8 E-15	2.7	11.02	8.14	.203
	364	13.81	2.74	3.4 E-25	2.1	11.48	8.11	.203
3	2	13.81	2.58	.051	2.12	11.43	8.11	.203
	100	14.87	.237	7.3 E-17	1.39	10.40	8.06	.202
	200	14.87	.237	1.2 E-29	.723	10.36	8.07	.202
	300	14.11	2.07	3.3 E-15	.396	10.98	8.13	.203
	364	13.84	2.73	4.1 E-25	.311	11.45	8.11	.204
4	2	13.84	2.57	.051	.309	11.40	8.11	.204
	200	14.89	.237	1.4 E-29	.106	10.35	8.06	.202
	364	13.84	2.73	4.15 E-25	.046	11.45	8.11	.204
5	2	13.84	2.57	.051	.045	11.39	8.11	.204
	200	14.89	.237	1.4 E-29	.015	10.34	8.06	.202
	364	13.84	2.73	4.17 E-25	6.6 E-3	11.45	8.11	.204

In a second simulation (Table 5.12), oxidation pond discharge was decreased by half over a period of 20 years. Under these conditions the *Chione* biomass decreased to a value 77% that of the original biomass after 20 years. All other parameters except suspended organic matter also decreased.

Table 5.12 Simulated decrease in nutrients and organic matter from the Bromley oxidation ponds; in the Avon-Heathcote Estuary yearly submodel.

Program changes: Oxidation pond discharge decreases by half over 20 years

PN goes from .55 → .27 (= .014 g yr^{-1})

PO goes from .5 → .25 (= .0125 g yr^{-1})

```
130  PN = .55
140  PO = .5
951  PN = PN - .014
952  PO = PO - .0125
```

Year	T	C	G	B	A	D	Y	E
1	2	32.93	12	.071	100.7	29.95	8.03	.776
	50	38.56	.226	.081	137.8	25.59	8.24	.802
	100	38.16	.006	.081	146.4	26.52	8.12	.833
	150	35.95	.006	.081	119.9	28.17	8.12	.858
	200	36.10	.006	.081	89.2	27.52	8.20	.860
	216	36.36	.006	.081	81.4	27.19	8.21	.859
	217	36.36	.061	.015	81.0	27.17	8.21	.858
	250	36.53	1.89	.017	69.7	27.03	8.21	.854
	300	36.74	4.67	.026	67.6	27.21	8.19	.840
	350	35.67	7.42	.029	89.3	28.4	8.16	.817
	364	36.05	5.48	.028	99.7	28.4	8.12	.811
2	2	36.04	4.84	.075	101.2	28.1	8.11	.795
	100	37.53	.083	.082	144.1	26.3	8.11	.818
	200	35.51	.083	.082	87.5	27.1	8.20	.843
	300	36.21	4.68	.014	65.8	26.9	8.18	.824
	364	35.57	5.48	.010	95.5	28.0	8.10	.797
3	2	35.55	4.84	.074	97.0	27.8	8.09	.782
	200	35.05	.084	.082	82.1	26.6	8.20	.827
	364	35.05	5.40	.003	87.7	27.6	8.10	.785
4	2	35.03	4.79	.074	89.0	27.4	8.09	.770
	200	34.65	.085	.082	73.9	26.1	8.20	.810
	364	34.50	5.35	.001	77.4	27.2	8.09	.774
5	2	34.48	4.75	.073	78.5	26.9	8.08	.760
	200	34.31	.087	.082	64.1	25.5	8.19	.793
	364	33.94	5.29	4.2 E-4	65.8	26.8	8.09	.764
6	2	33.92	4.71	.072	66.71	26.55	8.08	.749
	200	33.99	.089	.082	53.49	24.82	8.19	.776
	364	33.38	5.24	1.5 E-4	53.86	26.40	8.09	.754
7	2	33.36	4.66	.072	54.59	26.14	8.08	.739
	200	33.68	.090	.080	43.02	24.21	8.18	.760
	364	32.82	5.18	5.3 E-5	42.46	25.98	8.09	.743

.../Cont'd

Table 5.12 - Cont'd

Year	T	C	G	B	A	D	Y	E
8	2	32.80	4.62	.071	43.02	25.72	8.08	.729
	200	33.45	.092	.061	33.29	23.66	8.16	.743
	364	32.26	5.13	1.8 E-5	32.19	25.55	8.09	.732
9	2	32.24	4.58	.071	32.6	25.31	8.08	.717
	200	33.30	.094	.025	24.8	23.22	8.11	.727
	364	31.70	5.07	6.2 E-6	23.4	25.13	8.09	.719
10	2	31.68	4.53	.070	23.7	24.90	8.08	.705
	200	32.98	.096	7.3 E-3	17.7	22.73	8.08	.710
	364	31.14	5.01	2.6 E-6	16.3	24.71	8.09	.706
11	364	30.58	4.95	6.6 E-7	10.9	24.29	8.09	.692
12	364	30.03	4.89	2.1 E-7	6.9	23.86	8.09	.677
13	364	29.47	4.82	6.2 E-8	4.2	23.44	8.09	.662
14	364	28.91	4.76	1.8 E-8	2.4	23.01	8.09	.646
15	364	28.35	4.69	5.4 E-9	1.3	22.59	8.09	.629
16	364	27.80	4.63	1.5 E-9	0.7	22.16	8.09	.621
17	364	27.24	4.56	4.3 E-10	.34	21.73	8.10	.596
18	364	26.68	4.49	1.2 E-10	.16	21.31	8.10	.579
19	364	26.12	4.42	3.3 E-11	.07	20.88	8.10	.563
20	2	26.12	4.01	.064	.072	20.71	8.08	.548
	200	27.49	.123	2.7 E-10	.042	18.47	8.06	.542
	364	25.57	4.35	8.8 E-12	.030	20.45	8.10	.546

This case is the reverse of the nutrient enrichment that has occurred in the Avon-Heathcote Estuary through development of the drainage basin and increased nutrient loading by way of the oxidation ponds. These simulations indicate that a significant portion of the cockle population (perhaps as much as 58%) may be supported by the discharge from the Bromley Oxidation Ponds.

6 THE ROLE OF *C. STUTCHBURYI* IN THE ENERGY FLOW OF THE AVON-HEATHCOTE ESTUARY: A SYNTHESIS

Qualitatively, the cockle *C. stutchburyi* is a prominent member of the benthic macrofaunal community of the Avon-Heathcote and many other estuaries in New Zealand; reaching densities as great as 3,000 m^{-2} (section 2) and often dominating classical Petersen type community characterisation of mudflat areas (Knox & Kilner, 1973; Voller, 1973; Morton & Miller, 1973). However, little is known of the quantitative importance of this animal, in spite of the fact that; (1) it supports a traditional recreational fishery and has recently become part of the commercial shellfishery, and (2) it is an animal of wide distribution in areas subject to increasing environmental pressure and may be valuable as an indicator species. In addition, it is representative of a niche common to most estuarine systems (the filter feeding infaunal bivalve mollusc); and the importance of the role of members of this niche has been stressed many times but has been quantified inadequately.

In the previous sections, *C. stutchburyi* has been shown to be abundant over most of the mudflat area of the Avon-Heathcote Estuary. Biomass and net production values (calculated on an ash-free dry weight basis from Tables 4.2 and 4.3) are within the range presented for other bivalve populations by a variety of authors (Table 6.1). The P:B ratio (actually Pg:B in this case) is calculated to be .03 and .12 for maximum and minimum estimates of these parameters respectively. *C. stutchburyi* lives considerably longer than the other bivalves listed in Table 6.1 and the low Pg:B ratio for this species is consistent with the generalisations of Waters (1969) that animals with shorter life histories have higher P:B ratios on an annual basis.

Robertson (1979) presented an equation relating annual P/B ratios and lifespan for bivalve molluscs ($\log_{10}$ P/B = 0.621 + (-.783) $\log_{10}$L; where L = lifespan in years). *C. stutchburyi* would be predicted to have a P/B ratio of 0.4; approximately four times the value calculated in this study.

The role of *C. stutchburyi* as the major filter feeding benthic mollusc has been defined. Energy is collected from several sources, in the form of suspended particulate organic matter, and distributed along several paths. Particulate matter filtered, but not assimilated is directed through pseudofaeces and faeces to the detrital and decomposer

Table 6.1 Values of biomass (B) and production of body tissue from recent studies of intertidal bivalves, expressed as g AFDWt m^{-2} or g dry wt m^{-2} (*).

Species	B	P_g	P_g:B	Reference
Chione stutchburyi	18 - 377	2 - 14		This study
Cerastoderma edule	18 - 65	29 - 71	1.1 - 2.6	Hibbert (1976)
Mercenaria mercenaria	8 - 50	4 - 14	0.2 - 0.5	Hibbert (1976)
Mya arenaria	5.5	2.7	0.5	Warwick & Price (1975)
Scrobicularia plana	2.1	0.5	0.2	Warwick & Price (1975)
**Macoma balthica*	1.3	1.9	1.5	Burke & Mann (1974)
**Mya arenaria*	4.6	11.6	2.5	Burke & Mann (1974)
**Mytilus edulis*	3 - 15	4 - 20	1.3	Burke & Mann (1974)
Venerupis pullastra	135	20	0.15	Johannessen (1973)
Mytilus edulis	125 - 400	268		Milne & Dunnert (1972)
Scrobicularia plana	5 - 40	3 - 13		Hughes (1970)

food chains. That assimilated is passed through flesh to predators and decomposers; or through shell to a very slow recycling by decomposers and weathering.

C. stutchburyi assimilates particulate organic matter of terrestrial, marine and autochthonous origin (section 4.8.2). In the area inhabited by cockles (4.5×10^6 m^2), assimilation is estimated to be between 5.65×10^2 and 6.1×10^3 kJ m^{-2} yr^{-1} and to sustain a population with a biomass of 17.8 to 369.6 g m^2 (equivalent to 3.5×10^2 - 7.4×10^3 kJ m^{-2}), an organic production of 41.9 to 260.9 kJ m^{-2} yr^{-1} and a total yearly production (P+R) of 434.8 to 5.5×10^3 kJ m^{-2} yr^{-1} (Table 4.9).

Energy flow through the *C. stutchburyi* population, expressed on an areal basis for the entire estuary is summarised in Table 6.2.

In order to quantify the role of this species in the system or to assess importance of the animal, the relationship between the cockle and other components of the estuary must be compared in some manner. However, interpretation of significance or importance is a grey area and there are no standard methods of assessment.

Table 6.2 Energy flow through *C. stutchburyi* of the Avon-Heathcote Estuary on an areal basis (area of the estuary = 6×10^6 m^2).

(1)	Winter biomass	13.6	to	283.3	g AFDWt m^{-2}
	energy content	270	to	5.7×10^3	kJ m^{-2}
(2)	Net production (body growth)	1.6	to	10.3	g AFDWt m^{-2} yr^{-1}
	energy	32.2	to	200	kJ m^{-2} yr^{-1}
(3)	Available flesh	12	to	76.7	kJ m^{-2} yr^{-1}
(4)	Reproduction	110	to	2.3×10^3	kJ m^{-2} yr^{-1}
(5)	Mortality		200		kJ m^{-2} yr^{-1}
(6)	Total production	3.3×10^2	to	2.7×10^3	kJ m^{-2} yr^{-1}
(7)	Respiration	96.7	to	2000	kJ m^{-2} yr^{-1}
(8)	Assimilation	433	to	4.7×10^3	kJ m^{-2} yr^{-1}

The importance or significance of the benthic community in general is indicated by the number of flows interacting with that compartment. The degree of "connectivity" has been used as a measure of the relative association of donor and recipient compartments for whole ecosystem matrices by Patten (1975) and Dame *et al.* (1977); and similarly may indicate the importance of compartments in energy flow models. In the present case (Fig. 5.3) the macrobenthic invertebrate module, dominated by *C. stutchburyi* has the greatest connectivity and thus may be hypothesised to be of major importance to energy flow through the system.

The magnitude of energy flow along different pathways has been used to show their relative importance (see for example Rosenberg *et al.*, 1977). Similarly, it was of interest to calculate the proportion of the total Avon-Heathcote energy that was associated with *C. stutchburyi*.

As has been discussed in section 5.1, energy at different levels of an ecosystem is of different quality, and not strictly comparable without the use of a "quality factor" (H.T. Odum & E.C. Odum, 1976). Energy quality factors are defined as the ratio of the heat equivalent energy produced or upgraded by a system to the quantity of energy required

to power the system (Alexander *et al.*, 1980; H.T. Odum & E.C. Odum, 1976). Energy quality ratios for physical energies have been reported and used in several publications (H.T. Odum *et al.*, 1978; H.T. Odum, 1978); however, the embodied energy of animal components of ecosystems has not been adequately documented and there are theoretical problems associated with calculation of quality ratios in the conventional manner.

From the definition and from the values calculated in this study, the quality factor for *C. stutchburyi* may be calculated as follows:

$$\frac{\text{total solar energy}}{\text{energy of } C.\ stutchburyi} = \frac{4.97 \times 10^5 \text{ kJ m}^{-2} \text{ yr}^{-1}}{2.7 \times 10^3 \text{ kJ m}^{-2} \text{ yr}^{-1}} = 184.$$

When multiplied by the energy in *C. stutchburyi* in the normal manner, this factor results in a solar equivalent energy value for cockles that is equal to the value of incoming sunlight. Calculation of quality factors for animal communities seems to have been neglected in the literature on energy analysis; the only ones being those of H.T. Odum *et al.* (1978) and Wang *et al.* (1980) calculated in terms of the genetic content of species and concerning survival of populations.

Jansson & Zucchetto (1978) and others have used heat equivalent energy to compare the energy flow through the biotic components of ecosystems. Energy flow values for *C. stutchburyi* are compared with those calculated for the Avon-Heathcote Estuary in Table 6.3. Maximum estimated cockle production represents 3.0×10^{-5}% of the total energy flow through the Avon-Heathcote Estuary (both expressed in heat equivalents).

Table 6.3 Comparison of estimates of total energy entering the Avon-Heathcote Estuary, and that involving *C. stutchburyi*.

Total energy (heat equivalents) through the Avon-Heathcote Estuary (Table 5.1)	8.9×10^9 kJ m^{-2} yr^{-1}
Total energy (solar equivalents)	3.0×10^{14} kJ$_{SE}$ m^{-2} yr^{-1}
Chione stutchburyi	
energy content (biomass)	5.7×10^3 kJ m^{-2}
max total production	2.7×10^3 kJ m^{-2} yr^{-1}

This involvement in total energy flow appears to be very small, but of course it must be remembered that most of the total energy of the Avon-Heathcote Estuary is physical energy. Although the input of particulate organic matter to the Avon-Heathcote Estuary has not been measured, the rapid rate of filtration of water by the cockle population (water turnover time of 0.6 to 375 hours, section 4.8) plus the fact that *C. stutchburyi* redirects almost all ingested matter (either through pseudofaeces or its own energy budget) indicates that *C. stutchburyi* is probably involved with a high proportion of the total organic energy flow.

As the major filter feeding bivalve, *C. stutchburyi* may be assumed to account for a major part of the biodeposition in the estuary. As in the case of *Mercenaria* (Hibbert, 1977b) a significant portion of the consumed energy is deposited in the sediment, so that *C. stutchburyi* may be supporting more than its own production, again, in detritus-based deposit feeding groups.

The natural components of the estuarine system will have evolved in accordance with the existing available energies of the system. According to the maximum power principle (Lotka, 1922; H.T. Odum, 1971a, 1973, 1975; Welch, 1977), those species and systems survive which are best able to capture and utilise energy for the creation and maintenance of adaptations to existing environmental conditions (Jansson & Zucchetto, 1978).

The energy signature of the Avon-Heathcote Estuary has changed drastically since settlement of the drainage basin by man (section 1.2). The total input of energy to the estuary has increased, especially because of organic matter imported to the drainage basin and subsequently cycled through the estuary by way of the Bromley Oxidation Ponds. In addition, the distribution of energy has changed. The Bromley Ponds account for a very large proportion of the total energy input now, and river flows have been altered. *C. stutchburyi* has survived these changes, and is probably more abundant than before.

The study of energetic models has led to the conclusion that the magnitude of flux (energy or biomass) per unit standing crop through a system, or the power capacity, is positively correlated with the system's resilience (O'Neill, 1976; De Angelis *et al.*, 1978; De Angelis, 1980). E.P. Odum (1975) in comparing diversity and stability of ecosystems concluded that the quality and quantity of energy inputs determined the level of diversity; that low diversity was characteristic of, and presumably

optimal for, systems (such as estuaries) in which one or a few sources of high utility energy are subsidised by high quality auxiliary energy flows and/or large nutrient inputs.

C. stutchburyi has remained viable in the Avon-Heathcote Estuary in spite of great environmental perturbations; probably due to its ability to utilise a variety of suspended particulate organic food types. As is typical of high energy/low diversity systems, the Avon-Heathcote Estuary has been temporally stable in its fauna and reasonably resistent to perturbations while receiving regular or consistent energy inputs. The tendency to a "boom and bust" situation with fluctuating energy subsidies (predicted by E.P. Odum, 1975) has been realised in the blooms of *Ulva*, and probably a higher biomass of cockles with increased oxidation pond discharge.

In a system of low diversity and high energy, all species are important in terms of energy flux and ecosystem stability. *C. stutchburyi* is concluded to be especially so, perhaps not through the magnitude of its total energy flow (which has been hard to compare quantitatively) but (at least) by virtue of its high connectivity with the rest of the system and its intimate association with the particulate organic matter food chain.

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Avon-Heathcote
Estuary under stress

Estuaries

Many of New Zealand's estuaries are surrounded by cities, which have harmful effects upon the ecosystem. Rob Stephenson of the Zoology Department, Canterbury University, gives an historical account of the effects of the growth of Christchurch on the Avon-Heathcote Estuary, and looks at the levels of pollution it can handle

Rob Stephenson

The Avon-Heathcote Estuary is a small (6 km² in area) bar-built estuary, with a drainage basin of approximately 200 km² (Fig 1). During the past 130 years, the City of Christchurch has grown around it — to the present population of approximately 300,000. Consequently, over 80% of the freshwater catchment is heavily urbanised.

The effect that urban and industrial development around the estuary has had upon the estuarine ecosystem has been significant, and is the subject of this case study.

The Avon-Heathcote Estuary has, in characteristic fashion, reflected the drastic alteration of its drainage basin by changes in its own physical, chemical and biological characteristics. Changes in vegetation, drainage patterns and land cover altered the nature and degree of flow characteristics and sedimentation. In addition, the domestic and industrial effluents discharged into the rivers and into the estuary proper have had far-reaching effects upon the kinds and numbers of plants and animals within the estuary. In parallel with these man-induced changes, there have been the naturally occurring, short-term changes in the configuration of the spit, the outlet channel and the channels within the estuary — all characteristic of estuarine instability.

Settlement of the drainage basin

European settlement of the drainage basin began in the 1850s. At that time, flats forming the catchments of the two rivers and their tributaries were largely areas of swamp. Raupo and flax were dominant, interspersed with tussock grass, fern, tutu and patches of swamp forest dominated by kahikatea. Early maps indicate many shallow ponds and shaking bogs, drained by a dense network of small meandering streams and separated from the sea by a belt of low dunes.

Growth of the city was rapid, both in terms of population and in the area of the drainage basin urbanised (Fig. 2a). As the population grew, the quality of the watershed surface water deteriorated to the point where, after rain, the area was often a '... pestilential swamp'. Although early drainage works were undertaken by the Canterbury Provincial Council, it was not until 1878 (after the formation of the Christchurch Drainage Board) that an organised start was made on an underground stormwater and sewage system. The effluent from this system was subjected to primary treatment at the Bromley Sewage Farm, before being discharged into the estuary. This resulted in improved quality of surface water, and in 1890 the Colonial Analyst reported that water entering the

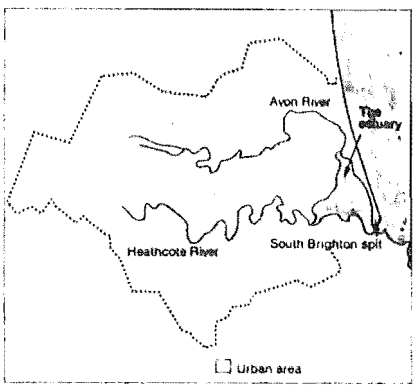
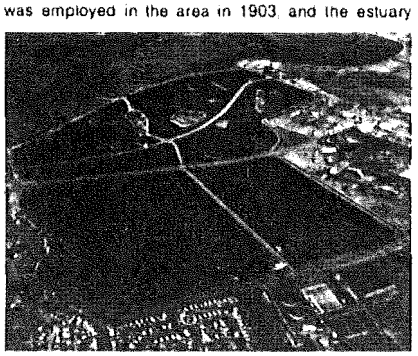


Figure 1. The Avon-Heathcote Estuary

estuary from the sewage farm was '... deprived of any harmful constitutents'.

By 1901, 54 km of pipes were laid (Fig. 2b) and 12.1 million litres of effluent flowed daily into the sewage farm. A side effect of the sewage system was a change in the surface runoff characteristics of the drainage basin. By 1930, a minimum of 7200 litres per hectare per day of ground water entered the sewers from the city area, reducing surface runoff from unpaved areas as a result.

Although the sewage farm served the city itself, untreated domestic effluent entered the estuary from several surrounding housing areas. Most significant, however, was the discharge of industrial effluents directly into the estuary and its rivers. The area of Woolston, along the banks of the Heathcote River, became the most heavily industrialised area of New Zealand. One fifth of the total New Zealand work force was employed in the area in 1903, and the estuary



The Bromley Sewage Works and the western side of the estuary

Estuaries

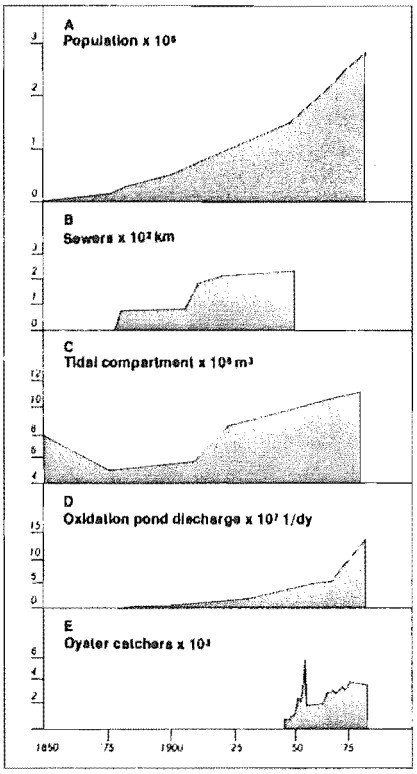


Figure 2. Events in the Avon Heathcote Estuary and its drainage basin 1850-1980. (A) population of Christchurch (B) length of sewers (kms). (C) volume of the tidal compartment. (D) volume of effluent discharge from the Bromley Sewage Works. (E) winter resident numbers of the South Island pied oystercatcher.

received the — often untreated — effluent from factories including woollen mills, rubber factories, a gelatine and glue factory, woolscouring works, a fellmongery and a starch factory.

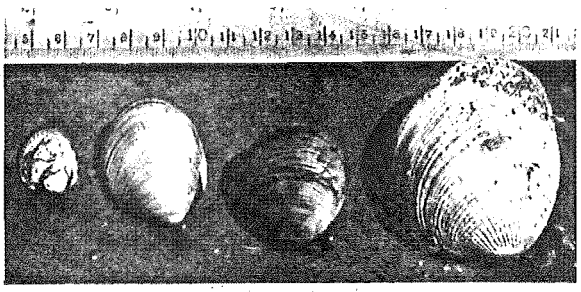
In 1926, the sewage farm system was replaced by the two-stage system of the Bromley Sewage Purification Works. Primary treatment was followed by secondary treatment — by biological oxidation — in a series of ponds, before the effluent was discharged into the estuary. After 1950, there was a gradual diversion of some industrial effluents into the city sewage system for treatment (Fig. 2d). Industrial sewers and pumping stations were built connecting industrial areas with the sewage works. In 1971, with the completion of the Woolston industrial sewer and Pumping Station No 15, almost all industrial discharges into the Heathcote River ceased.

Changes in the estuary

The rapid urban growth and accompanying change in vegetation cover with early settlement appear to have resulted in an increase in sediment supply to the Avon and Heathcote Rivers. The sediment was deposited in the estuary as a 50-60 cm thick layer of distinctive mud, and this resulted in a decrease in the tidal volume of the estuary by an estimated 30% between 1850 and 1875 (Fig. 2c).

It is reasonable to assume that this deposition of a thick layer of fine sediment over a short period of time would have stressed the benthic invertebrate community immensely: there is evidence that large mature populations of the bivalves *Chione stutchburyi* and *Mactra trishs* were killed by this deposition. In addition, the increased load of suspended sediment may have reduced light penetration in the estuary and decreased primary production. However, this may have been accompanied by an increase in the detritus supply. The change to sediments of very fine particle size would have made it very hard for filter feeding bivalves to exist, but it would have favoured certain deposit feeding forms such as polychaetes.

After 1875, sediment yields were reduced owing to improvements in drainage of the city area and



*A large shell of the cockle **Chione stutchburyi** (right) thought to have existed before settlement of the drainage basin compared with shells from three present populations.*

increased impervious cover (roofs and roads), which altered runoff characteristics. The estuary responded with an increased tidal compartment to a present volume which is slightly greater than that of 1850, and which appears to be approaching stability. The estuary remains a net exporter of sediment.

Encroachment of urban development on the rivers and estuary led to reclamation of a great deal of the bordering high tide wetlands. Main river channels leading into the estuary have been widened and straightened, and most of the perimeter of the estuary is now sea wall, or has some form of shore protection. Most notably, McCormacks Bay was separated from the estuary by a causeway, which severely restricted flow and changed the tidal regime. The bay was then partially filled in during a reclamation project.

The first biological study of the Avon-Heathcote Estuary was carried out in 1928-9. At this time a few changes which had occurred in the fauna were evident. The bivalve *Mactra trishs* was represented by very few small living individuals, though large beds of shells of dead individuals were recorded. The whitebait *Galaxias attenuatus*, which was "at one time

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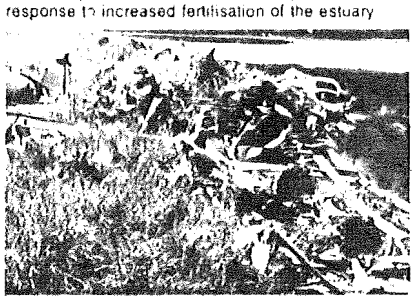
Estuary under stress

Estuaries

common and bred in the estuary', had been severely reduced in number, and it was reported that now only scattered individuals are taken. Shells of the cockle *Chione stutchburyi* were reported as being thin and fragile, with an incidence of 60% infection by a burrowing polychaete worm. It appears that the living individuals of both *Mactra tristis* and *Chione stutchburyi* were at that time — and still are today — much smaller than those which had inhabited the estuary at some time previously. Although only a small amount of chemical analysis was undertaken in the 1928-9 survey, it showed a marked decrease in dissolved oxygen concentration with distance 'upstream' in the estuary, especially toward the Heathcote River.

A second survey of the Avon-Heathcote Estuary, undertaken in 1951, reported that 'large areas of the mudflats about the main effluent, starch factory effluent and St Andrews Hill effluent, harbour a specialised fauna composed of only a few species. The restricted fauna in these areas indicate the presence of decaying organic matter derived from the effluents.' The animal life in the rest of the estuary seemed unchanged from the earlier survey, although counts of the mud snail *Amphibola crenata* showed an increase in number. What was significantly different, however, was the change in flora of the estuary. Blooms of the alga *Ulva lactuca* were apparent, whereas the earlier survey had referred to '... a little *Ulva* in sheltered rock pools and on muddy sand banks'. Presumably these were a response to increased fertilisation of the estuary.



Rubbish dumped into one of the few remaining patches of high tide wetlands. A convenient area for infilling and waste disposal?

These trends continued into the 1970s. Areas near the mouth of the Heathcote River and the oxidation pond outfall exhibited anaerobic conditions and a marked restriction in community diversity — and blooms of *Ulva* continued. By the early 1970s, the Bromley Works were handling virtually all of the city effluent, including industrial wastes. In 1973, it was estimated that the sewage works contributed 80% of the nitrogen and 94% of the phosphorus entering the estuary — far outweighing the natural load (Fig. 3).

The improved treatment and removal of all but the occasional — accidental or otherwise — discharge of industrial effluent into the Heathcote River has improved the state of the estuary. The high BOD load of the Heathcote River has been reduced. This was estimated to be the equivalent of one third of the BOD of the Bromley oxidation ponds, released into 1.5 km of the river, in 1971. This reduction, together with the

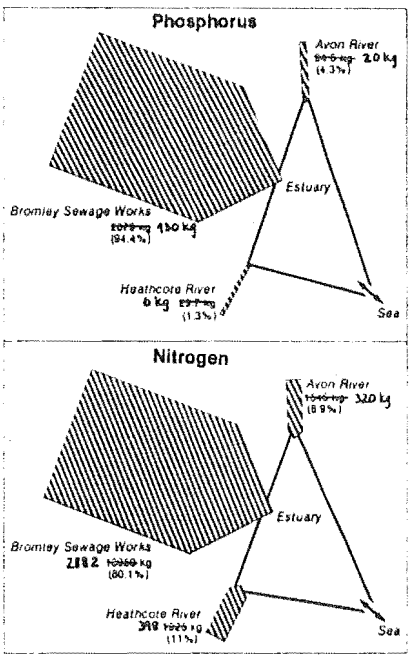


Figure 3. The relative contributions of total phosphorus and nitrogen to the Avon-Heathcote Estuary from the Bromley Sewage Works, the Avon River and the Heathcote River.

practice of allowing discharge from the oxidation ponds only on the outgoing tide (so that more of it goes out to sea rather than ponding around the outfall), has improved conditions around the effluent sites and has effectively reduced the nutrient load on the estuary. Whitebait has recently returned in catchable numbers and the algal blooms have not been as severe in the last few years.

The estuary has also experienced the introduction of the cordgrass *Spartina* x *townsendii*, and an astounding increase in the numbers of the South Island pied oystercatcher which it supports (Fig. 2e). These events are not related to urbanisation of this particular drainage basin, but are associated with post-European settlement changes in New Zealand as a whole.

An assessment

Effluent discharge into the Avon-Heathcote Estuary had two components — toxic chemicals and organic matter. Toxic industrial pollutants entered mainly the Heathcote River and included arsenic and cromium compounds (from tanneries), hydrochloric acid (glue factories), acids, alkalis and sulphur compounds (woollen mills), bisulphate of lime (wool scours), acids, copper, and lead (metalworks etc.), and tars and oils (gas works). These types of compounds, if not lethal, can have serious sublethal effects on aquatic

Estuaries

organisms. They affect reproduction or growth and often, as in the case of metals, can be concentrated in animals because of their mode of feeding. This component of effluents is not tolerated at all well by the estuarine system. Consequently it is little wonder that, while raw industrial effluent was flowing into the Heathcote River, the biological reports of the river and the area around its mouth were bleak.

The organic fraction of the effluents, on the other hand, has an effect of steadily fertilising the system. While the high BOD loads of mass discharges at specific sites cause localised anaerobic conditions, the general response curve to increased effluent — especially treated effluent reduced to nitrates and phosphates — is represented in Fig. 4. In most natural systems, an increase in nutrients — or eutrophication — will be accompanied by an increase in production to a maximum, followed by a decline.

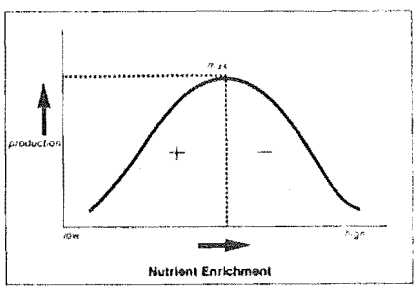


Figure 4. A generalised response curve showing production with nutrient enrichment.

It is difficult to estimate just where the Avon-Heathcote Estuary lies with respect to this curve. Computer simulation models of *Chione* populations indicate that as much as 30% of the *Chione* production may be supported by oxidation pond effluent. Certainly, the response exhibited by the algae *Ulva* of increased blooms with increased effluent discharge, and subsequent decline with greater treatment of effluent, indicates that the estuary was still on the positive side of the curve (Fig. 4). It appears as if the Avon-Heathcote Estuary was moving toward a eutrophic condition until very recently, and has now started moving away again. In general terms, urbanisation of the drainage basin of the estuary has shifted major paths of energy flow. Urbanisation has added an external source of energy to the system, and the main flow of energy is now through the oxidation ponds.

Between human activities and the natural system of the estuary, ecological associations develop and are modified because of special interactions. The addition of wastes stresses many components of estuarine systems, but some species adapt to the new conditions forming an 'interface system'. In the history of the Avon-Heathcote Estuary, such interface systems developed naturally at the mouth of the Heathcote River and around effluent discharges — noted as large numbers of a few tolerant species. But more recently, such an interface system has been created artificially in the oxidation ponds formed at the Bromley Sewage Works, and this has taken a load off the estuary proper. The recognition and domestication of interface systems, as a way to reduce environmental impact, is becoming a principle in coastal zone management.

Scientific study and management

The Avon-Heathcote Estuary is unique amongst New Zealand estuaries in having had biological investigations carried out as early as 1928-9. These have established a base line, against which the numerous more recent studies could be compared. Most significant in terms of estuary management was the completion in 1973 of a comprehensive report *The Ecology of the Avon-Heathcote Estuary*, prepared for the Christchurch Drainage Board by the Estuarine Research Unit, Department of Zoology, University of Canterbury. The report not only assessed the biological, physical and chemical state of the estuary, but it also established goals and objectives for future management.

Too often, estuaries have been considered as a resource with a single, primary use and have been manipulated and altered without care or thought being given to the other uses they should serve. Interested users and controlling authorities of the Avon-Heathcote Estuary have begun to appreciate that the estuary must be regarded as a resource with multiple uses: a drainage basin to receive the stormwater drainage of the City of Christchurch; a receiving area for the disposal of effluent from the Bromley Sewage Works; a nursery area for flounders and other fish; a valuable feeding area for seasonal and migratory birds; an increasingly important body of water for sport and recreation; a recreational fishery; an educational resource and area for scientific study; a vital area of 'open space' in the City of Christchurch; and, not the least, a unique ecosystem that provides aesthetic enjoyment. Not all of these uses are compatible, but any management decisions must take all possible uses and values into account. Under the City of Christchurch district planning scheme (2nd Review, December 1979) the estuary receives its own recreation zone classification.

Although the Avon-Heathcote Estuary has been markedly altered in some respects, it appears still to be fulfilling its natural role — such as a nursery ground for flounder etc. Aspects of the change which has taken place, such as increased nutrient load, are reversible — as has been demonstrated. Others, however, such as the loss through infilling of high tide wetlands, are not. It is hoped that no vital parts of the estuarine ecosystem have been lost altogether, and it is presumed that future guided management of the remaining natural estuarine areas will succeed in retaining enough intact, so as not to change the estuarine diversity.

Most of the data and many of the theories presented here have been compiled over a number of years by a succession of people working on aspects of the Avon-Heathcote Estuary. In particular I wish to acknowledge the work of Professor G. A. Knox and members of the Estuarine Research Unit, Department of Zoology, University of Canterbury, and of Dr J. M. Macpherson, formerly of the Department of Geology, University of Canterbury.

APPENDIX II

THE UNIVERSITY OF AUCKLAND

PRIVATE BAG AUCKLAND NEW ZEALAND TELEPHONE 792-300

Department of Zoology
1 October 1979

Mr R. Stephenson
Zoology Department
University of Canterbury
Private Bag
CHRISTCHURCH

Dear Rob,

Enclosed is a print for you of the Chione stutchburii specimens in the Banks collection now in the British Museum in London. These were the first to be collected by Europeans. This shell collection is described by G.L. Wilkins, "A catalogue and historical account of the Banks Shell Collection" Bull. Brit. Mus. (Nat. Hist.), Historical Series 1(3); 69-119, 1955.

The handwriting in the collection is that of Solander. To quote Wilkins (p. 97): "Chione stutchburii, frequently attributed to Gray, was first figured by William Wood (1828 Index Testaceologicus: Supplement iv +59 pp. London; pl. 2, fig. 4) from a specimen in the British Museum."

Now, I have seen the types in the British Museum, distinct from the Banks lot. There are three specimens on a plaque labelled "from ~~Sandwich Island~~, New Zealand", with a gummed-on label on reverse "Chione stutchburii Gray mc"

Stutchburii is obviously a manuscript name of Gray, and was then used by Wood, who figured one of these specimens. The identity of the person putting the label on the back was possibly Mrs Gray (see Dance "Shell collecting, an illustrated history" Faber 1966). The mc refers to Cuming, who was an avid but not accurate accumulator of shells (and barnacles) who got his localities+labels mixed up. One of Cuming's collectors was a Mr Jukes, whose name appears with New Zealand barnacles, mislabelled from Australia, and which Darwin had access to after they had been deposited in the British Museum.

So, the Solander shells, of Endeavour origin, although referred to in MSS (p. 162)

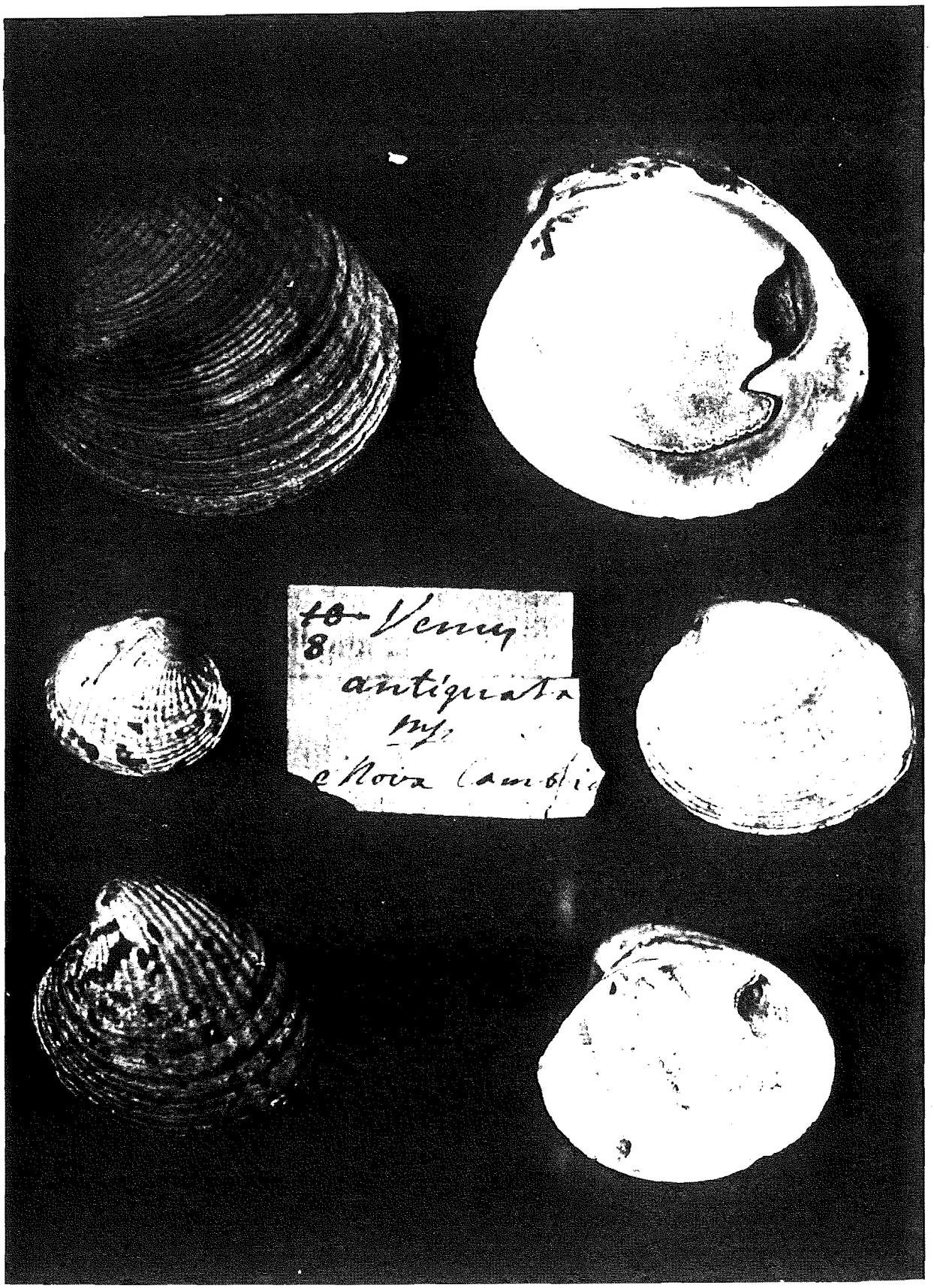
antiquata VENUS ovalis sub cordat ~~elasticis~~,
striata longitudinibus sulcata (....) etc
MCPgB MB Habitat in Oceano pacifico, Nova Cambrinn
alicante JB.

transcript of Solander's manuscript.

became lost to science, and subsequently the Cuming's mislabelled ones were the first to be published about (by Wood). Hope this is of a little interest.

formerly Cantrus

Brian A. Foster


to Venus
8
antiquata
Inf.
e Nova Cambria

APPENDIX III

Ministry of Agriculture & Fisheries

P.O. BOX 2298 WELLINGTON
NEW ZEALAND

DFI BUILDING
110 FEATHERSTON ST
PHONE 720 367

Fisheries Management
7, Donald McLean Street
Wellington. Tel. 892-15

September 19 1980

Mr Rob Stephenson
Department of Zoology
University of Canterbury
CHRISTCHURCH 1.

Dear Mr Stephenson,

I write in reply to your letter of 18 August 1980 enquiring about cockles.

...Enclosed is a list of landing data provided from our central statistics section whose data is based on information supplied by fishermen. The column headed "value" is, I believe, derived from approximate values derived some time ago but at 20 cents/kilo it hardly seems valid? I have not been able to verify actual prices for cockles in 1979.

To the best of my knowledge the declared landings deal solely with Chione stutchburyi of which the overwhelming majority is harvested by hand picking.

I understood some two years ago that a device was being developed for suction-dredging for cockles in the Auckland area but I have no knowledge of its eventual use.

I cannot say how many permits are issued for harvest of cockles since M.A.F. issues permits for the method of fishing involved - i.e. hand picking - and such permits will apply to hand picking of pipi, paua, cockles, etc. Also since the information supplied on fishing returns is confidential I may not say how many of the permits were actually utilised or what their respective catches were.

The data on 'port of landing' reflects the office which issued the fishing permit and not necessarily the area where the fish were taken: for example, the cockles declared as from Tauranga, Opotiki and Whakatane probably all come from Ohiwa harbour.

Restrictions may be placed on permits for harvesting shell fish and may specify areas where harvesting is prohibited, size limits and quotas.

For the Ohiwa harbour fishery no minimum size limit is specified but each permit is limited to a maximum catch of eight sugar bags per week (each contains approximately 750-800 cockles) Slightly different quotas may apply to permits issued in other areas for other cockle fisheries.

I believe that some of the cockles are eventually canned, some used in soup manufacture, etc, but many are simply sold in the shell in hotels, etc. I know of potential export markets for cockles in various parts of the world but do not have any data to hand on current export volumes - if any. Perhaps Department of Trade and Industry could help you with this last information. — exports probably minimal -

I trust the above limited data is of use to you.

Finally, may I suggest you contact Mr Ron Blackwell of Auckland University who is currently working on cockles at Ohiwa harbour in pursuit of a Ph.D.

Yours faithfully,

A R Branson

(A.R. Branson)
for Director
Fisheries Management Division.

...Encl.

ANDREW R. BRANSON
Fisheries Mangement Lab.
7, Donald McLean Street
Wellington. Tel. 832-159

COCKLE

1977

PORT OF LANDING	WEIGHT - KG.	VALUE — Questionable.
WHANGAREI	1,760 KG.	$ 387
TAURANGA	2,625	577
WHAKATANE	405	89
NAPIER	5	1
KAIPARA	5,798	1,275
LYTTELTON	81	18
TOTAL:	10,674 KG.	$ 2,348.

1978 — ?

PORT OF LANDING	KG	VALUE
WHANGAREI	80	$ 17
AUCKLAND	181	40
MANUKAU	3,000	660
TAURANGA	2,685	591
OPOTIKI	9,416	2,071
NEW PLYMOUTH	2	—
LYTTELTON	201	44
AKAROA	11	2
GREYMOUTH	18	4
TOTAL:	15,594 KG.	$ 3,431

1979 — ?

PORT OF LANDING	KG	VALUE
WHANGAREI	2,758	$ 606
AUCKLAND	360	79
THAMES	11,610	2,554
MANUKAU	18,968	4,173
TAURANGA	1,125	247
OPOTIKI	15,763	3,469
GOLDEN BAY	20	4
TOTAL	50,604 KG	$ 11,134

ANDREW R. BRANSON
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19/9/80

APPENDIX IV

CHRISTCHURCH STAR, Wed., January 24, 1979 3

Deadly peril in shellfish

Don't eat shellfish—containing potentially deadly viruses — from the Estuary, says the Health Department

The warning came from the deputy-medical officer of health in Christchurch (Dr M. A. Brieseman) after reports that people were gathering shellfish in the area during the weekend.

Dr Brieseman said the city's oxidation ponds, emptying into the estuary, removed most bacteria from sewage but viruses could not be traced in the effluent.

People eating shellfish from there ran the risk of contracting typhoid, cholera and bowel diseases, some of them deadly.

No cases of illness related to shellfish consumption had been reported recently and there were no cases of typhoid or cholera in the city.

There was no law stopping people from taking the shellfish but those who did should make sure they were well cooked, Dr Brieseman said.

Fisheries regulations stopped people from marketing shellfish from the area.

People could also contact hepatitis from eating uncooked shellfish taken from the area and this disease is contagious.

Hepatitis was now the most common notifiable disease in the city.

Some with the disease had followed normal hygiene practices but had been paddling in the water, he said.

Because shellfish filtered vast quantities of water, bacteria and virus concentrations in them were high.